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Stapeliads

of Southern Africa and Madagascar
Volume II



by Peter V. Bruyns
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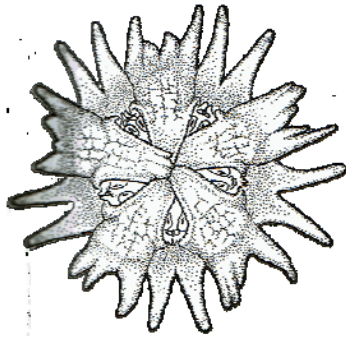
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New combinations published in this work

Australluma ubomboensis
Duvalia caespitosa subsp. *pubescens*
D. caespitosa subsp. *vestita*
Huernia barbata subsp. *ingae*
H. blyderiverensis
H. guttata subsp. *reticulata*
H. hislopilii subsp. *cashelensis*
H. hystrix subsp. *parvula*
H. verekeri subsp. *angolensis*
H. verekeri subsp. *pauciflora*
H. zebrina subsp. *insigniflora*
Larryleachia cactiformis var. *felina*
Orbea longii
Pectinaria longipes subsp. *villetii*
Piaranthus cornutus var. *ruschii*
P. geminatus subsp. *decorus*
P. punctatus var. *framesii*
Stapelia grandiflora var. *conformis*
S. hirsuta var. *baylissii*
S. hirsuta var. *gariepensis*
S. hirsuta var. *tsomoensis*
S. hirsuta var. *vetula*
S. paniculata subsp. *kougabergensis*
S. paniculata subsp. *scitula*
Tromotriche pedunculata subsp. *longipes*

11. Pectinaria



Pectinaria was established by Haworth in 1819 for the single species *Stapelia articulata*. Sweet modified the concept of the genus somewhat by moving *Stapelia mammillaris* to Pectinaria, although N. E. Brown (1890) later placed this species in *Caralluma*. J. Decaisne (1844) placed both species in his section *Pecti-*

naria of *Stapelia*. The character of the genus was changed drastically by N.E. Brown (1907-09). He described four new species of *Pectinaria*, all of which were discovered by N.S. Pillans between 1902 and 1904. In so doing he redefined the genus so that the five species that were in it were held together only by the fact that their corolla lobes remained fused at their tips at anthesis, which gives the flower a bud-like appearance.

White & Sloane (1937) added little except an account of *P. tulipiflora* which had been described by Carl Lückhoff in 1934. In this 'species' the corolla lobes were sometimes free at the tips but sometimes remained fused there. In 1939 Pillans described *P. mirkinii*, in which the corolla lobes are always free at their apices. *Pectinaria breviloba* was described in 1954 and *P. stayneri* in 1975 and in both of these the corolla lobes are mostly fused at their tips. Bayer & Plowes (1975b) reviewed the position in *Pectinaria* and showed that the genus consisted of three groups of species which did not seem to be closely related. In 1978 the present author

described a further species, *P. exasperata*, in which the corolla lobes are also mostly free at their tips. By now it had become clear that *Pectinaria* in the sense of N.E. Brown was not a coherent entity and, as a consequence, it was split into three genera in Bruyns (1981a).

In this new arrangement, the two species *P. articulata* and *P. asperiflora* were kept in *Pectinaria* as subspecies of *P. articulata*. *Pectinaria arcuata* and *P. mirkinii* were moved to a new genus *Ophionella*, where they were placed under the single species *O. arcuata*. The remaining taxa were placed in *Stapeliopsis*. Recent studies have reinforced these conclusions and, in Bruyns (1999e), it was shown that *Pectinaria sensu* N.E. Brown is not monophyletic.

Originally Haworth named *Pectinaria* for the comb-like teeth of the outer corona and it was found that this is also present in two relatively little known species of *Caralluma*, *C. longipes* and *C. maughanii*. These species share several other characters with *P. articulata* and so they were moved into *Pectinaria* (Bruyns 1981a). In September 1999 the even more obscure

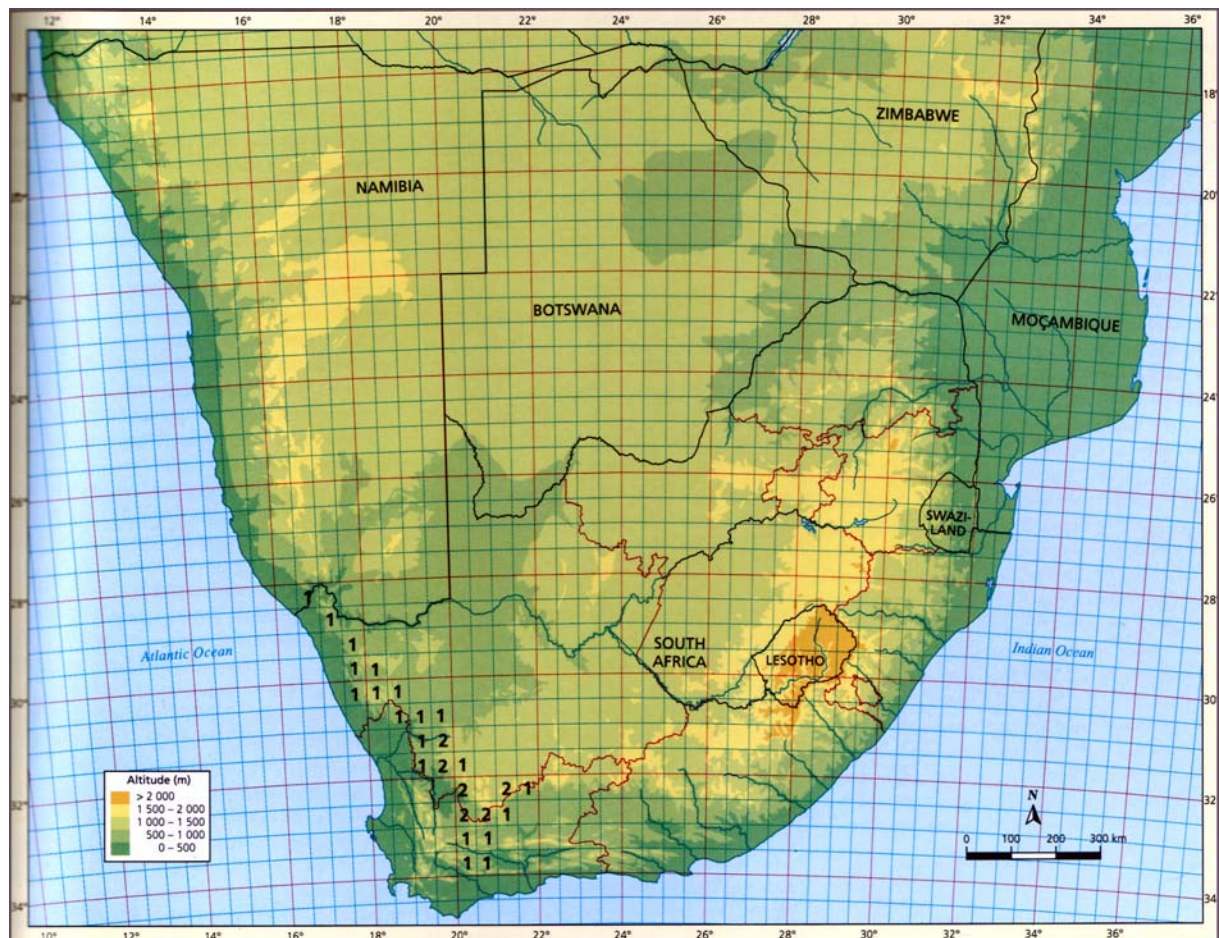


Fig. 11.1. Patterns of diversity in *Pectinaria*, showing the number of species recorded to date in each half-degree square.

Caralluma longipes var. *villetii* was recollected and that is now included and documented with illustrations in the present account. The resulting genus consists of three species and this entity has been shown to be monophyletic using morphological characters (Bruyns 1999e) and molecular data (Bruyns & Klak, in prep.).

Pectinaria Haw., *Suppl. Pl. Succ.* 14 (1819), *nom. cons.*

Stapelia sect. *Pectinaria* (Haw.) Decne, in DC, *Prodr.* 8: 663 (1844).

Type: *Pectinaria articulata* (Alton) Haw.

Vadulia Plowes, *Exceisa* 20:18 (2003).

Type: *Vadulia longipes* (N.E.Br.) Plowes.

Dwarf spineless non-rhizomatous succulent forming mat 60-300 mm diam. **Stems** 10-150 mm long, 10-25 mm thick, prostrate with upturned apex to decumbent, fleshy and firm, glabrous, green to purplish or blackish green, young tissue pinkish; **tubercles** 2-4 mm long, low pyramidal so that stem subtessellate, spreading, slightly laterally flattened and joined towards base into 6 obtuse angles along stem, tapering into small often slightly hardened acute tooth-like leaf-rudiment, without stipular denticles. **Inflorescences** glabrous, 1-20 per stem, arising towards tips of stems between angles, each bearing 1 (-2) flowers usually subtended by single narrowly lanceolate acute bract < 1 mm long without lateral teeth, seated on small rounded tubercle; **pedicel** 2-35 mm long, 0.7-1.2 mm thick, erect to descending, often S-shaped; **sepals** 1.5-2.5 mm long, 1 mm broad at base, lanceolate, acute. **Corolla** 5-17 mm diam., ± rotate in Sect. *Erectiflora*, campanulate and bud-like in Sect. *Pectinaria*; outside glabrous, smooth in Sect. *Erectiflora*, papillate in Sect. *Pectinaria*; inside smooth in Sect. *Erectiflora*, densely papillate in Sect. *Pectinaria*; **tube** < 1 mm long and scarcely containing column in Sect. *Erectiflora*, 1.5-4.0 mm long, broadly inverted conical to hemispherical in Sect. *Pectinaria*; lobes spreading in Sect. *Erectiflora*, remaining joined at tips and incumbent over tube in Sect. *Pectinaria*, ovate-lanceolate to lanceolate, mostly convex inside from reflexed to recurved margins, margins eiliate. **Corona** 1.0-1.5 mm tall, 2.0-2.5 mm broad, glabrous, consisting of 2 series of lobes arising on staminal tube and partly intergrown, raised above base of tube on short stout obtusely pentagonal stipe: **outer lobes** 0.5-1.0 mm long, bifid for about half of length into slightly diverging, narrowly deltoid ± erect terete horns, joined laterally in lower half to bases of inner lobes and forming pouch around guide-rails, with ridge behind inner lobes divided into numerous spreading to erect, finger-like lobules in series with outer lobes and together with them forming comb-like ring; **inner lobes** 0.25-0.50 mm long, adpressed to backs of anthers, dorsiventrally flattened, ± deltoid but sometimes much reduced. **Anthers** horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** ellipsoidal, broader than long, pellucid margin exactly along outer edge, caudicle attached with small ± circular pad to ventral surface. **Follicles** erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

As in several other genera (e.g. *Stapelia* and *Quaqua*), plants are very readily recognised as belonging to the genus *Pectinaria*. They form dense mats containing large numbers of stems that are prostrate with upturned apices and have no tendency at all towards being rhizomatous. The stems are cylindrical and their surface is divided by low but clearly defined tubercles which are more or less square in outline and arranged into six angles along the stem. This is achieved by having two alternating whorls each consisting of three tubercles. Young growth has a noticeably pinkish colouring in the terminal bud, and the lower surface of the stems in contact with the ground is also often pinkish. Older growth is dark green and becomes blackish if very exposed. The stems of all species are edible, possessing a consistency and taste somewhat like lettuce and devoid of the bitter after-taste that is common to many stapeliads.

The leaf-rudiment on these stems is reduced to a cylindrical to slightly flattened point that is undifferentiated from the tubercle and without stipules.

Under the electron microscope, the surface of the stem in *Pectinaria* turns out to be quite interesting. It is papillate and these papillae are gathered into raised islands with fairly deep crevices between them (fig. 18 C). There is much variability across the genus in this convolution of the surface, with the most extreme forms being found in some subspecies of *P. articulata*. In *P. longipes* the surface is less dramatically convoluted, and in *P. maughanii* the surface is much flatter.

In *Pectinaria* the primary stem does not bear flowers. These are borne towards the tips of the stems on new growth and virtually never appear on older stems. There are usually many inflorescences per stem. Except in *P. maughanii* (where two flowers may occasionally develop on a single inflorescence), each inflorescence consists of a single flower and a single bract (fig. 21 B). The bract is usually seated on a swollen, raised cushion and is narrow, without lateral outgrowths.

All species of *Pectinaria* have small flowers. In *P. articulata* the corolla lobes are joined at the tips so the flower has a peculiar bud-like shape at maturity. In the other two the flower is more or less flat, with free and spreading lobes. The flowers seem to be scentless.

In *P. articulata* the outside of the corolla is papillate. On closer examination (here it must be very close - this is only seen easily with the electron microscope), each of these papillae is found to consist of five or six epidermal cells raised into a hill with a stoma at its summit (fig. 25 D). Examination with the light microscope shows that the inside of the corolla is covered with a fantastic landscape of raised papillae whose surfaces are themselves covered with finer papillae (each of which is the outer wall

of a single cell) so that each larger papilla resembles a rough pine-cone. The apical cell of each large papilla is different from the others but is much smaller than the papilla (unlike in *Huernia* where it is often larger). The surface of the flower in *P. longipes* and *P. maughanii* is dull by comparison, both inside and outside, and completely without any papillae.

The corona is very similar in all three species. The whole structure is relatively broad and flat and rests on a short pedestal. It is contained within a small tube at the centre of the flower so as to be roughly flush with its surface. The outer corona lobes are erect to spreading and deeply bifid into narrow, cylindrical teeth opposite the guide-rails. They continue as a raised, ridge-like dorsal process which is finely divided into erect to spreading finger-like lobules behind each inner lobe. The outer lobes therefore form a shallow cup around the column, which has deeper bays opposite the guide-rails and is shallowest behind the anthers. The small inner lobes are dorsiventrally flattened and adpressed to the anthers, sometimes meeting in the centre of the style-head.

The pollinaria in *Pectinaria* are particularly small. Here the pollinia are quite a bit broader than long and the insertion-crest lies exactly along the shorter side. The corpuscle and caudicles are also minute.

As in *Quaqua*, the seeds of *Pectinaria* are boat-shaped, uniformly brown and papillate all over.

Pectinaria is found only in the western part of South Africa (fig. 11.1). The distribution coincides almost exactly with the western edge of the escarpment from Fraserburg westwards and northwards to the high peaks of the Richtersveld in the north-west. The genus occurs mostly just west of the edge of the Karoo dolerites. Only *P. articulata* subsp. *asperiflora* is found below the escarpment in the south-eastern parts of the Ceres Karoo and at the western edge of the Little Karoo. *Pectinaria articulata* and *P. longipes* are sometimes found growing together around Sutherland and also occur close to one another near Loeriesfontein.

Although occasionally found on steep slopes, specimens of *Pectinaria* are usually encountered in flat areas of very uniform appearance. Here they shelter under small bushes of the asteraceous shrubs *Pteronia*, *Erioccephalus* or *Pentzia* or clumps of spiny, gregarious species of *Ruschia*. Plants generally grow well hidden under the nurse-plant, frequently in quite substantial accumulations of leaf-litter and partially decayed organic debris, in soft, easily penetrated soil.

I. *Pectinaria* sect. *Pectinaria*

Pedice short, holding flower close to stem. **Corolla** bud-like at anthesis with lobes remaining joined at tips; outside papillate, inside densely covered with obtuse conical to hemispherical papillae.

In this section the flowers frequently open in dark places under bushes, they are small and often held close to the ground, and have narrow entrances. Consequently, it is possible that they are pollinated by small gnats which might move around only in such sheltered, relatively dark places. No scent has been detected in the flowers but this might only be a result of a lack of careful observation.

Key to the sections

- Inside of corolla papillate, lobes joined at tips **I. Sect. *Pectinaria***
 Inside of corolla not papillate, lobes free at tips **II. Sect. *Erectiflora***

1. *Pectinaria articulata*

Pectinaria articulata (Aiton) Haw., *Suppl. Pl.*

Succ.: 14 (1819).

Stapelia articulata Aiton, *Hort. Kew.*, ed. 1, 1: 310 (1789)

Type: South Africa, Cape, Roggeveld, *Masson & Thunberg* (missing).

Neotype: Masson, *Stap. Nov.*: t. 30 (1797).

Stems 5-150 mm long, 12-25 mm thick, prostrate usually with upturned apex; tubercles tapering to soft or sometimes slightly hardened point. **Pedice** 1.5-15.0 mm long 0.75-1.25 mm thick, usually spreading, often slightly fluted towards apex; **sepals** 2.0-2.5 mm long, acute **Corolla** 5-8 mm long, 5-11 mm diam., bud-like, truncate and flat-topped to conical, maroon to cream inside and outside; outside with scattered obtuse papillae; inside densely covered with translucent crystalline bristly papillae increasing in length towards centre of flower to each max. at level of corona lobes then abruptly disappearing towards base of tube behind corona; **tube** 1.5-5.0 mm long, broadly and shallowly conical to hemispherical, containing gynostegium; **lobes** 4-6 mm long, incumbent over tube and joined at tips leaving only narrow openings between them to inside of flower, $\pm$ deltate, with margins folded back so that strongly convex inside. **Corona** $\pm$ 1.5 mm tall, 2-3 mm broad, bright yellow to dark maroon, raised on obtusely pentagonal stipe up to 0.5 mm long; **outer lobes** 0.5-1.0 mm long, erect to spreading, bifid in upper half into terete obtuse slightly diverging lobules, laterally fused in lower half to bases of inner lobes, pectinate portion behind inner lobes with ridge of horizontally spreading to ascending obtuse teeth; **inner lobes** 0.3-0.5 mm long, deltoid, obtuse to truncate.

This species occurs over the whole distribution of the genus with the other two sympatric with it. It is very variable, especially in the shape of the corolla and even such apparently distinctive taxa as subsp. *articulata* may be difficult to distinguish from others such as subsp. *namaquensis* on occasion. Four allopathic subspecies are recognised. The most distinctive and least variable of them is subsp. *asperiflora* which occupies the southernmost part of the distribution.

All these taxa have peculiarly bud-shaped flowers in which the corolla lobes remain joined at their tips, leaving quite small, narrow openings between them through which access to the flower can be obtained. The inside is covered with crystalline papillae which make these otherwise dull and drab flowers quite remarkably beautiful under a dissecting microscope. Since the shape of the corolla may be unreliable, the shape of the outer walls of the epidermal cells on these papillae is the main way of separating the subspecies.

Both subsp. *articulata* and subsp. *namaquensis* occur in cream- and purple-brown-flowered forms. In subsp. *articulata* there is a gradual gradation from the one to the other, but in subsp. *namaquensis* these two colour forms are geographically isolated.

Key to the subspecies of *P. articulata*

1. Corolla lobes bent back to meet within or at mouth of tube **1a. subsp. *articulata***
1. Corolla lobes meeting well outside mouth of tube **2.**
2. Papillae in tube covered with acute cells **3.**
3. Corolla 3-5 mm long, inside uniformly cream to pale greyish yellow or maroon **1c. subsp. *namaquensis***
3. Corolla 4-8 mm long, inside maroon to cream finely speckled with maroon **1b. subsp. *asperiflora***
2. Papillae in tube covered with obtuse cells **1d. subsp. *borealis***

1a. *Pectinaria articulata* subsp. *articulata*

Pectinaria flavescens Plowes, *Excelsa* 20:17 (2003).

Type: 3 km south-west of Calvinia, *Plowes* 7419 (SRGH).

Pedice 1.5-15.0 mm long, $\pm$ S-shaped and holding flower facing upwards. **Corolla** 2.5-5.0 mm long, 5-8 mm diam. (broadest at mouth of tube), flat-topped with lobes bent back into tube; outside cream to pale grey-green usually irregularly lined with pale maroon; inside maroon to pink or cream, with conical obtuse papillae 0.25-0.60 mm tall covered with obtuse cells and sometimes with an elongated apical hair; **tube** 2.5-5.0 mm long, 5-8 mm broad at mouth, hemispherical to slightly conical; **lobes** 4-5 mm long, 3-4 mm broad at base, depressed into tube, meeting in tube or near mouth, convex from reflexed margins. **Corona** dark maroon to pale yellow; **outer lobes** ascending, with pectinate portion behind inner lobes usually spreading.

Distribution and habitat

Subsp. *articulata* is not common except in a small area to the north-west of Sutherland where it sometimes occurs with *P. longipes*. As can be seen from the distribution map, it also occurs east of Sutherland to the south-west of Fraserburg, and at the easternmost known locality was found to be fairly plentiful.

Plants generally grow under small asteraceous shrubs of *Eriocephalus*, *Pentzia* or *Pteronia glomerata* in flat, slightly gravelly areas.

Diagnostic features and relationships

Both cream- and maroon-flowered forms exist of subsp. *articulata*. Plants from around the foot of the Hantam Mountains to the west and south-west of Calvinia have flowers where both

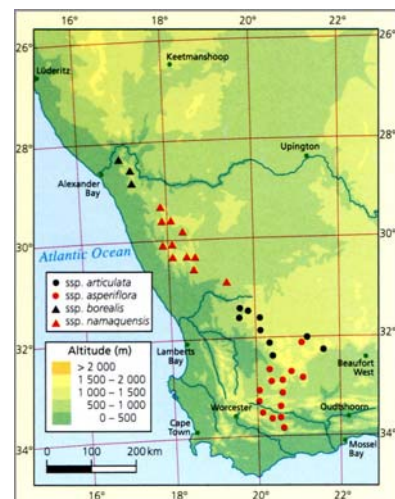


Fig. 11.2. Distribution of *Pectinaria articulata*.

PECTINARIA ARTICULATA



Fig. 11.3. *P. articulata* subsp. *articulata*, Heunis, near Middelpos.

the inside and the outside are cream. Nearer to Middelpos the colour of the flower is pale pink inside. North-east of Calvinia and from Middelpos southwards plants produce altogether darker flowers. Here the outside is pale grey-green with thick, vein-like markings of pale maroon. The inside is deep maroon.

In subsp. *articulata* the inside of the corolla is densely covered (except in the tube behind the corona) with crystalline, translucent-white papillae which are quite large relative to the size of the flower. In this subspecies the epidermal cells on these papillae have outer walls which project from the surface and are round-tipped. In dark-flowered plants the corona is dark maroon whereas in cream-flowered ones it is pale yellow, in both cases closely matching the colour of the flower.

This subspecies is usually clearly distinguishable from the others by the manner in which the flower faces upwards and by the peculiar, truncated appearance caused by the lobes bending back into the tube and joining at their tips within the tube. This arrangement is already obvious in the buds some time before they open. Unfortunately, neither of these characters is completely reliable. It has been found

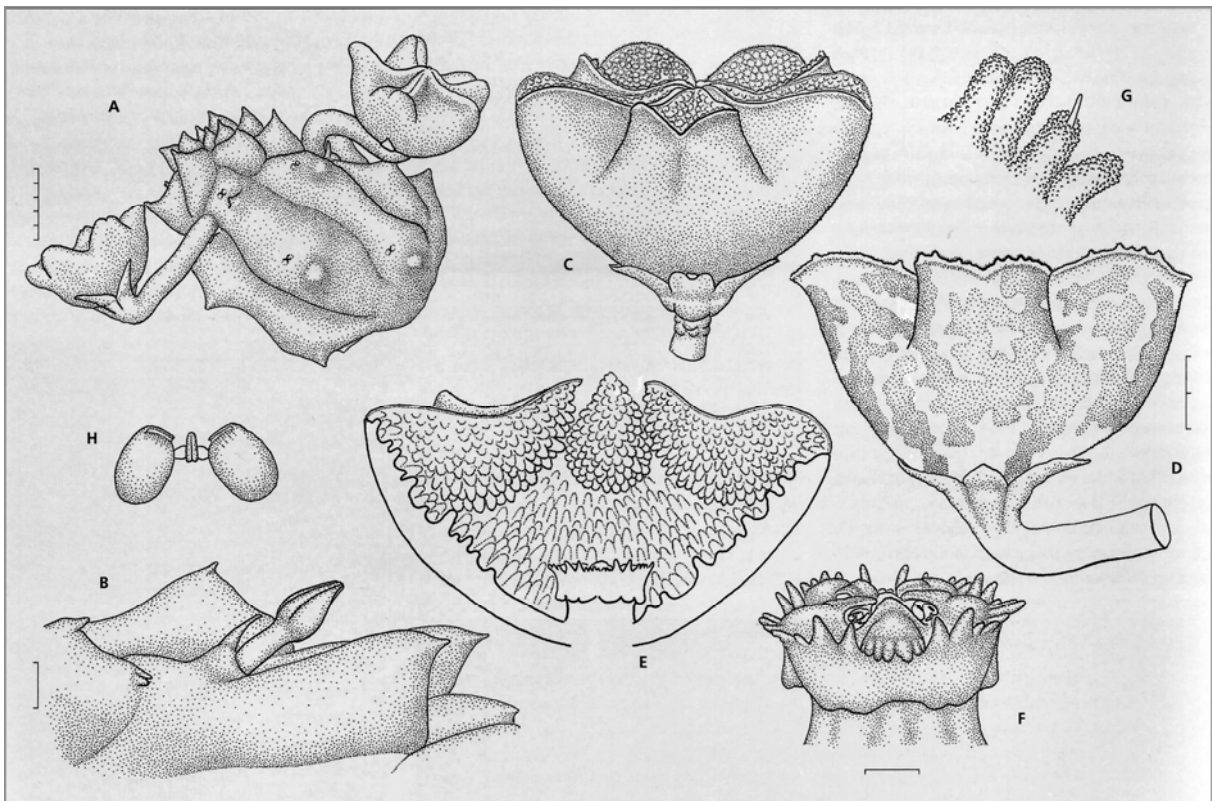


Fig. 11.4. *Pectinaria articulata* subsp. *articulata*. A, young stem with flowers. B, inflorescence. C, D, side view of flower. E, side view of dissected flower. F, side view of gynostegium. G, papillae inside corolla. H, pollinarium. Scale bars: A, 5 mm; B, E, 1 mm (at B); C, D, 2 mm (at D); F, 0.5 mm; G, 0.5 mm (at D); H, 0.25 mm (at D). Drawn from: D, Heunis, near Middelpos (no specimen); rest, Heunis, 5 km north of Sutherland (no specimen).



Fig. 11.5. *P. articulata* subsp. *articulata*, PVB 7971, north-east of Calvinia.



Fig. 11.6. *P. articulata* subsp. *articulata*, PVB 4281, north-west of Middelpos, plant with pinkish flowers.



Fig. 11.7. *P. articulata* subsp. *asperiflora*, PVB 4336, west of Calvinia. In this area most plants have cream-coloured flowers.

that flowers of the cream-coloured form have the lobes meeting sometimes within the tube, sometimes at the mouth and very occasionally slightly outside the tube.

History

Subsp. *articulata* was discovered by Francis Mason and Carl P. Thunberg in November 1774 during their joint expedition to the Han-tamberg and the Roggeveld. Masson introduced material to Britain in 1774, where it was described by William Aiton in the 1st edition of *Hortus Kewensis*, an account of the plants in cultivation at the time in Kew Gardens. Masson also figured material from his collection in his book *Stapeliae Novae*. After this, subsp. *articulata* remained uncollected until it was rediscovered by Rudolf Marloth on the Roggeveld, north-west of Sutherland, just before 1920.

lb. *Pectinaria articulata* subsp. *asperiflora*

Pectinaria articulata subsp. *asperiflora*

(N.E. Br.) Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 65 (1981).

Pectinaria asperiflora N.E. Br., *Fl. Cap.* 4 (1): 871 (1909).

Type: Cape, 2 miles north-west of Matjiesfontein, N.S. Pillans 70 (K, holo.; BOL, iso.).

Pedice 5-15 mm long, spreading ascending or erect then decurved towards tip, holding flower facing downwards. **Corolla** 4-8 mm long, 6-10 mm diam. (broadest just beyond mouth of tube), bud-shaped; outside faintly speckled with maroon on cream background to $\pm$ uniformly maroon; inside maroon to cream finely speckled with maroon (usually paler maroon to cream towards edge of lobes), with conical obtuse papillae 0.25-0.40 mm tall covered with acute cells; **tube** 2-4 mm long, 5-6 mm broad at mouth, broadly conical; **lobes** 4-6 mm long, $\pm$ 3.5 mm broad at base, joined at tips 2-5 mm outside mouth of tube into conical (sometimes broadly conical or somewhat flattened) structure, convex from reflexed margins. **Corona** maroon; **outer corona** ascending, pectinate portion behind inner lobes ascending to erect.



Fig. 11.8. *P. articulata* subsp. *asperiflora*, 38 km north-east of Montagu. Plant in habitat, wrapped around the bases of the stems of a small shrub of *Eriocephalus*, August 1978.



Fig. 11.9. *P. articulata* subsp. *asperiflora*, PVB 4841, south-west of Fraserburg.

Distribution and habitat

Subsp. *asperiflora* is found from the south-eastern edge of the Ceres Karoo eastwards along the margin of the Great Karoo from Matjiesfontein to south-west of Merweville. It also grows in the Little Karoo from the eastern foot of the mountains east of Montagu to around the base of the Warmwaterberg and the Anysberg. North of Matjiesfontein it grows within 5 km of populations of *P. longipes* and on one farm near Fraserburg both it and subsp. *articulata* have been collected. *Pectinaria longipes* has also been collected nearby, but of each taxon only a single plant was found so they are all extremely rare in this area.

Plants generally grow in flat, relatively low-lying areas and are often associated with Dwyka tillite. In many localities this subspecies occurs in the shelter of spiny shrublets of the gregarious *Ruschia spinosa* or *R. cradockensis*.



Fig. 11.10. *P. articulata* subsp. *asperiflora*, PVB 5278, northern foot of Anysberg.

Diagnostic features and relationships

In subsp. *asperiflora* the pedicel always holds the flowers facing downwards. They have a fairly prominent conical tube and the corolla lobes meet some distance beyond its mouth. The shape of the corolla is very variable, with the lobes sometimes quite steeply ascending from the tube but in other cases more horizontally inclined over the mouth of the tube. There seems to be less variation in colour than in most of the other subspecies and the flowers are generally maroon inside and a bit paler outside. The papillae inside the corolla are as large as those of the typical subspecies but differ in that the cells covering them have sharply acute rather than round-tipped outer walls.

History

Subsp. *asperiflora* was discovered by N.S. Pillans in January 1904 very close to Matjiesfontein. Although it is now known to be quite widespread and fairly common in places, it was next recorded only in 1948 by R.H. Compton.

1c. *Pectinaria articulata* subsp. *namaquensis*

Pectinaria articulata subsp. *namaquensis*

(N.E. Br.) Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 66 (1981).

Pectinaria articulata var. *namaquensis* N.E. Br., *Fl. Cap.* 4(1):871(1909).

Pectinaria namaquensis (N.E. Br.) Plowes, *Excelsa* 20: 17 (2003).

Type: Cape, Namaqualand, Templeman sub N.S.

Pillans 22 (K, holo.: BOL, iso.).

Pedicel 2-1.5 mm long, spreading with deflexed to upturned apex, holding flower facing downwards to horizontally to upwards. **Corolla** 3-5 mm long, 5-8 mm diam. (broadest just beyond mouth of tube), bud-shaped; outside greyish yellow to greyish maroon; inside cream to pale greyish yellow or maroon, with dome-like to conical obtuse papillae 0.15-0.30 mm tall covered with acute cells; **tube** 1.5-2.0 mm long, 2-4 mm broad at mouth, broadly conical and sometimes pentagonal; **lobes** $\pm$ 4 mm long, 3-4 mm broad at base, remaining joined at tips 2-3 mm outside mouth of tube into broadly conical structure, convex from strongly reflexed margins which may touch towards tip of lobe. **Corona** maroon or deep yellow; **outer lobes** ascending, pectinate portion behind inner lobes ascending.

Distribution and habitat

Subsp. *namaquensis* is confined to the western perimeter of Bushmanland and the eastern, drier flanks of the Kamiesberg. It has been collected from around Kliprand to north-east of Springbok and there are some isolated populations around Loeriesfontein. It is rather scantily recorded over this area but is not uncommon, especially around Gamoep.

Around the Kamiesberg it always grows on gneissic soils with a covering of fine gravel, mostly in flat areas and more rarely among rocks on top of hills. Populations of this subspecies are almost always associated with the vast colonies of *Ruschia divaricata* that are often found in the flats between the gneiss hills of this area. They are also occasionally found under shrubs in colonies of *R. robusta* or of *Eriocephalus*, mostly growing in deep shade and plenty of leaf-litter around the base of a bushlet.

In the area near Loeriesfontein it grows in flat spots under *Pteronia glomerata*, *R. spinosa* or other non-succulent shrublets on soils derived from shales.

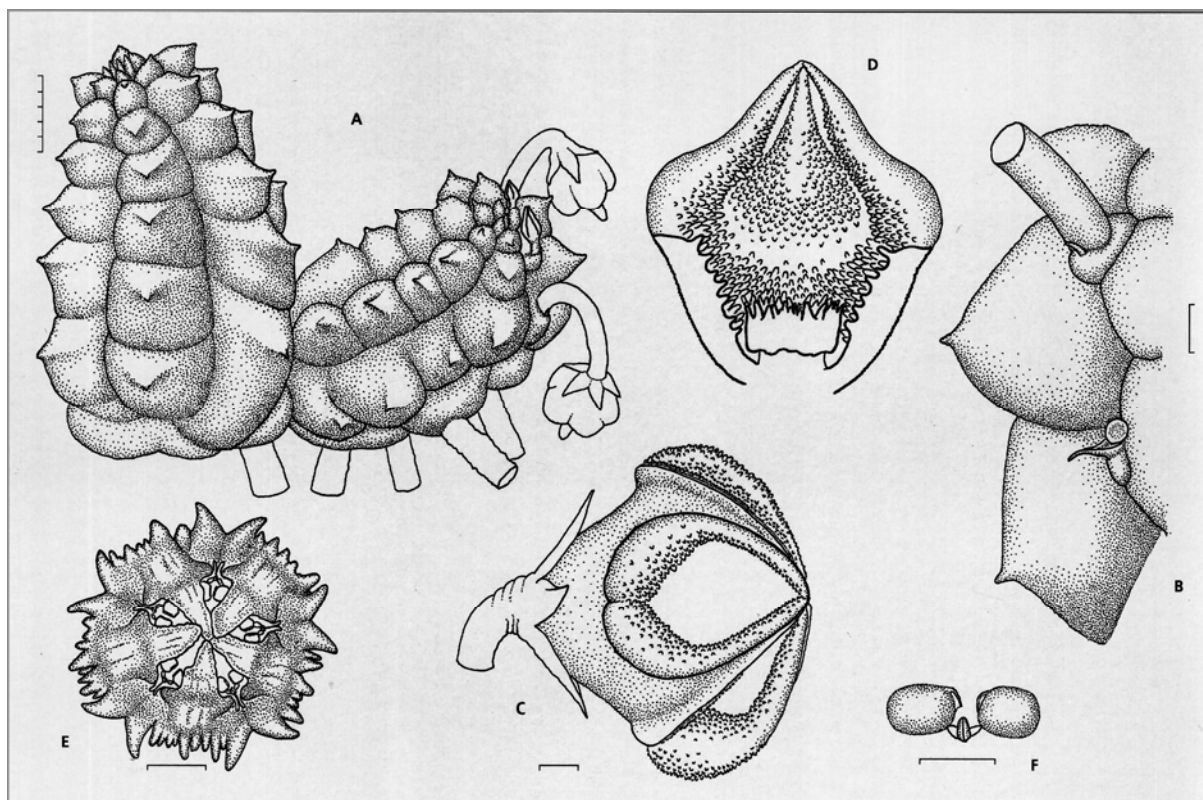


Fig. 11.11. *Pectinaria articulata* subsp. *asperiflora*. A, young stems with flowers. B, inflorescences. C, side view of flower. D, side view of dissected flower. E, face view of gynostegium. F, pollinarium. Scale bars: A, 5 mm; B, 1 mm; C, D, 1 mm (at C); E, 0.5 mm; F, 0.25 mm. Drawn from: A, B, D, E, *hort. W.C. Keen*; C, PVB 2938, 77 km north of Laingsburg; F, PVB 2940, 82 km north of Laingsburg.



Fig. 11.12. *P. articulata* subsp. *namaquensis*, PVB 4698, west of Gamoep, typical form with cream-coloured.



Fig. 11.14. *P. articulata* subsp. *namaquensis*, PVB 4698, west of Gamoep, typical form with cream-coloured flowers and pedicels of very variable length and orientation.



Fig. 11.15. *P. articulata* subsp. *namaquensis*, PVB 1504, Loeriesfontein, form with dark-coloured flowers.

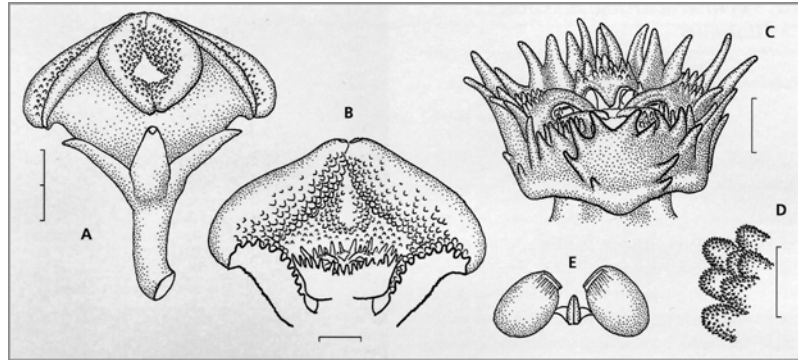


Fig. 11.13. *Pectinaria articulata* subsp. *namaquensis*. A, side view of flower. B, side view of dissected flower. C, side view of gynostegium. D, papillae inside corolla in tube. E, pollinarium. Scales: A, 2 mm; B, 1 mm; C, 0.5 mm; D, 0.5 mm; E, 0.25 mm (at D). Drawn from Kurzweil, Khiribes, Kamiesberg (no specimen).

Diagnostic features and relationships

In this subspecies the flowers are held facing in almost any direction on a pedicel of extremely variable length but which is sometimes as short as 2 mm long. The tube is particularly

short too and the united part of the corolla below the lobes is usually nearly flat with a small depression in the centre that contains the gynostegium. As a consequence, the flower is about twice as broad as it is long. The lobes converge and remain fused at their tips over the centre of the gynostegium. Their margins are well folded back (touching each other for some of their length) and, towards their bases, they project somewhat behind the flower.

Subsp. *namaquensis* is easily distinguished from subsp. *articulata* by the different shape of the flower and the acute cells on the papillae inside the corolla. From subsp. *asperiflora* it is less easily separated. The flowers again have a different shape (being far shorter with a particularly short corolla tube) and the papillae inside the corolla are broad and mostly dome-like, though some more conical ones have been seen and this character is not entirely reliable. As in the case of subsp. *asperiflora*, they are covered with sharp-tipped cells.

Two forms of this subspecies are known. One is found over the northern portion of the distribution. In this the flowers are cream with a bright yellow corona. The other form is known only on the plateau around Loeriesfontein. Here the flowers usually face upwards and are dark maroon to greyish (depending on how dark the papillae are) with a maroon corona. Although these forms are isolated from one another by some 80 km, there are no further significant differences between plants around Loeriesfontein and those found further to the north.

History

Subsp. *namaquensis* was discovered in Namaqualand in 1899 by Robert Templeman, who was a nurseryman in Rosebank in Cape Town.



Fig. 11.16. *P. articulata* subsp. *namaquensis*, PVB 1504, Loeriesfontein, form with dark-coloured flowers (but variable!).

PECTINARIA ARTICULATA

1d. *Pectinaria articulata* subsp. *borealis*

Pectinaria articulata subsp. *borealis* Bruyns,
Cact. Succ. J. Gr. Brit. 43: 67 (1981).

Pectinaria borealis (Bruyns) Plowes, *Excelsa* 20:17
(2003).

Type: Cape, Hellskloof, *Bayer 1506* (NBG).

Pedice 3-8 mm long, spreading then erect towards apex holding flower facing upwards. **Corolla** 3.5-7.0 mm long, 7.0-9.5 mm diam. (broadest just beyond mouth of tube), bud-shaped; outside greyish green to maroon; inside with conical obtuse papillae 0.15-0.30 mm long covered with obtuse cells; **tube** $\pm$ 2 mm long, 5 mm broad at mouth, broadly and shallowly conical; **lobes** 3.5-5.0 mm long, $\pm$ 4 mm broad at base, joined at tips $\pm$ 4 mm outside mouth of tube into broadly conical structure, strongly folded along middle so that margins touch towards tip. **Corona** maroon; **outer lobes** ascending, with lobules of pectinate portion behind inner lobes spreading.

Distribution and habitat

Subsp. *borealis* is found in the higher areas of the Richtersveld at between 600 and 1 300 m. It is known from between Kubus and Hellskloof in the west, from the Cornellsberg in the east and also occurs around Eksteenfontein.

At this altitude the rainfall is significantly higher than is typical in this otherwise very



Fig. 11.17. *P. articulata* subsp. *borealis*, PVB 8301, near Eksteenfontein, Richtersveld.

arid region and the average reaches 300 mm per year, compared with an average of 40-100 mm received annually for the low-lying parts of the Richtersveld (Anon 1966; Jürgens 1986: 177). Consequently the vegetation is very different from that found lower down. Plants of

subsp. *borealis* are usually found under small bushes of *Pteronia ciliata*, sometimes on gentle slopes but more often on plateaux and on flat-tish, stony areas where this species of *Pteronia* is dominant. They have often been seen in the company of *Euphorbia quadrata*.

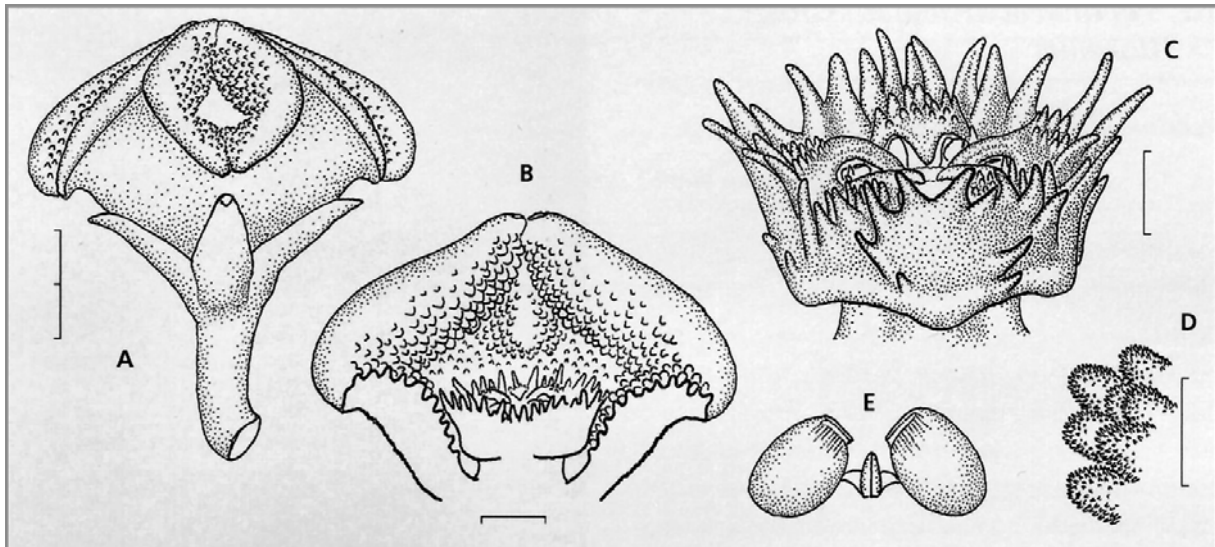


Fig. 11.18. *Pectinaria articulata* subsp. *borealis*. A, young stem with flower. B, inflorescence. C, side view of flower. D, side view of dissected flower. E, side view of gynostegium. F, papillae inside corolla in tube. G, pollinarium. Scale bars: A, 5 mm; B, D, 1 mm (at B); C, 2 mm; E, 0.5 mm; F, 0.5 mm (at C); G, 0.25 mm (at C). Drawn from PVB 3230, Cornellsberg.

Diagnostic features and relationships

As in the case of subsp. *namaquensis*, the flowers of subsp. *borealis* are about twice as broad as long. They have an almost flat to slightly conical 'tubular' area beneath the lobes in which there is a small depression in the centre which contains the gynostegium. The lobes are somewhat variable, sometimes with quite strongly reflexed margins, sometimes with the margins hardly reflexed at all. Usually the flowers are maroon but sometimes the papillae are transparent on this maroon background and this makes them appear much paler. The corona is maroon.

Subsp. *borealis* is probably most closely allied to subsp. *namaquensis* on account of the similarly conical flower. In subsp. *borealis* the papillae inside the flower are covered with obtuse cells and this readily distinguishes the two. In this latter feature it resembles subsp. *articulata*, but it can be distinguished by the shorter corolla tube and the different shape of the flower, in which the lobes are connate outside the tube.

History

This subspecies was first observed in 1977 by H.R. Tölken, E.G.H. Oliver and H.J.T. Venter in the course of their survey of the vegetation of some of the mountains of the Richtersveld, during which several new and unusual taxa were first observed. The first record was made by M. Bruce Bayer from plants that he found in 1977 Hellskloof in the Richtersveld.



Fig. 11.19. *P. articulata* subsp. *borealis*, PVB 8301, near Eksteenfontein, Richtersveld.



Fig. 11.20. *P. articulata* subsp. *borealis*, PVB 3940, Vanderserserrberg, Richtersveld, flowers with much paler papillae than in the previous ones.

II. *Pectinaria* sect. *Erectiflora*

Pectinaria sect. *Erectiflora* Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 63 (1981).

Type: *Pectinaria longipes* (N.E. Br.) Bruyns.

Pedice usually slender and holding flower well above stem. **Corolla** rotate with widely spreading lobes; outside and inside smooth (without papillae).

Key to the species

- Corolla lobes < twice as long as broad, corona deep yellow or red, inner lobes reduced and leaving most of backs of anthers exposed 2. *P. longipes*
Corolla lobes > twice as long as broad; corona dark purple-black, inner lobes covering anthers and often meeting in centre 3. *P. maughanii*

2. *Pectinaria longipes*

Pectinaria longipes (N.E. Br.) Bruyns, *Cact. Succ.*

J. Gr. Brit. 43: 69 (1981).

Caralluma longipes N.E. Br., *Fl. Cap.* 4 (1): 887 (1909).

Vadulia longipes (N.E. Br.) Plowes, *Excelsa* 20:19 (2003).

Type: South Africa, Cape, near Sutherland, fl. 1906, *Marloth* 3799 (BOL, holo.; PRE, iso.).

Stems 15-100 mm long, 10-20 mm thick, prostrate with upturned apices, green to brownish green; **tubercles** tapering into small acute rarely hard tooth. **Pedice** 4-35 mm long, 0.7-1.2 mm thick, erect holding flower facing upwards to erect becoming horizontal near apex to hold flower facing horizontally; **sepals** $\pm$ 2 mm long, shortly acute, slightly papillate beneath. **Corolla** 6-16 mm diam., rotate; outside pale green, smooth; inside yellow becoming slightly paler towards centre or pinkish, smooth; **tube** < 1 mm long, broad and shallow and just containing gynostegium; **lobes** 2.5-6.0 mm long, 1.5-3.0 mm broad at base, spreading, deltate to broadly ovate-deltate, acute, $\pm$ flat above with margins not or only slightly folded back. **Corona** 1 mm tall, 2.0-2.2 mm broad, deep yellow or red, raised on obtusely pentagonal stipe < 0.5 mm long; **outer lobes** $\pm$ 0.5 mm long, ascending, bifid (sometimes only notched towards apex) into narrowly deltoid to terete obtuse spreading to erect lobules, with pectinate portion behind inner lobes divided into numerous small spreading obtuse lobules or emarginate; **inner lobes** $\pm$ 0.25 mm long or less and so short as to leave most of backs of anthers exposed, deltoid, obtuse.

In many respects *P. longipes* and *P. maughanii* are similar. The main differences between them lie in the longer corolla lobes of *P. maughanii* (which are more than twice as long as broad) and the purple-black corona of *P. maughanii* in which the inner corona lobes cover the anthers completely. In *P. longipes* the inner corona lobes are much reduced and leave most of the backs of the anthers exposed. The flower in *P. maughanii* is also deep yellow with a purplish centre whereas in *P. longipes* it is always pale yellow.

The curious plant described by Carl Lückhoff as *Caralluma longipes* var. *villetii* is in a few respects intermediate between the two. The dimensions of the corolla, the corolla lobes and the corona lobes all correspond more closely to *P. longipes* than to *P. maughanii*. Similarly, the colours of the flower and the corona correspond more closely to *P. longipes* than to *P. maughanii*. In *P. longipes* the corolla usually faces horizontally and the corolla lobes are nearly completely flat whereas in 'var. *villetii*' the corolla faces upwards and the lobes are more convex inside. In these respects 'var. *villetii*' is similar to *P. maughanii*. Nevertheless, most of the features suggest that it is closer to *P. longipes* and because of its geographic separation it is treated here as a subspecies of *P. longipes*.

Key to the subspecies of *P. longipes*

- Flower facing horizontally, corolla 8-16 mm diam 2a. subsp. *longipes*
Flower facing upwards, corolla 6-8 mm diam 2b. subsp. *villetii*

PECTINARIA LONGIPES

2a. *Pectinaria longipes* subsp. *longipes*

Pedice 10-35 mm long, holding flower facing horizontally. **Corolla** 8-16 mm diam.; **lobes** 2.5-6.0 mm long, 2.5-3.0 mm broad at base, deltate to broadly ovate-deltate, usually uniformly yellow to pinkish in centre, margins usually not at all folded back.

Distribution and habitat

Pectinaria longipes subsp. *longipes* is mainly found on the Roggeveld plateau, occurring to the north-west, west and south of Sutherland, where it is most common. Plants have also been found in the eastern Roggeveld between Sutherland and Fraserburg but they are very rare in this area. There are a few scattered records from some of the higher ranges west and south of the Roggeveld plateau: in the Klein Roggeveld about 80 km south of Sutherland and in the Koedoesberge westward towards Ceres.

Plants are found in flat, sometimes gravelly areas (rarely on slopes), under *Erioccephalus*, *Pteronia* or other low-growing asteraceous shrublets.

Diagnostic features and relationships

In subsp. *longipes* the flower is borne on an often disproportionately long pedicel. This is erect and can be as long as 35 mm, in which case it holds the small flowers well above the stem. Near the end the pedicel bends so that the flower faces more or less horizontally. The flowers are usually around 10 mm across and so are relatively small, though of a size typical of the genus. When fully open they are almost flat. The inside is a dull yellow that often becomes slightly paler towards the centre. As is typical of this section, it is quite devoid of papillae, though it is not at all shiny. In *P. longipes* the short corolla lobes are ovate-deltate and the margins are not folded back strongly.

In most flowers seen, the small gynostegium in the centre has been yellow but the corona lobes can be red as well. In all specimens examined, the inner corona lobes were much reduced to a minute deltoid ridge around the bases of the anthers, leaving most of the anthers exposed on top of the gynostegium.

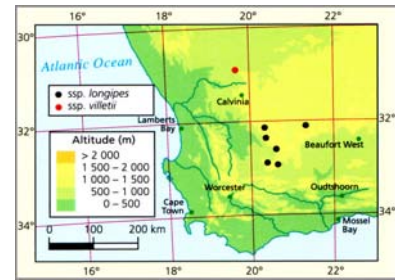


Fig. 11.21. Distribution of *Pectinaria longipes*.

History

Subsp. *longipes* was discovered by Rudolf Marloth in 1905 somewhere near Sutherland. It was rediscovered by Frances Leighton north of Matjiesfontein in 1954 but even today it has been rarely collected and remains one of the most poorly known of all the southern African stapeliads.

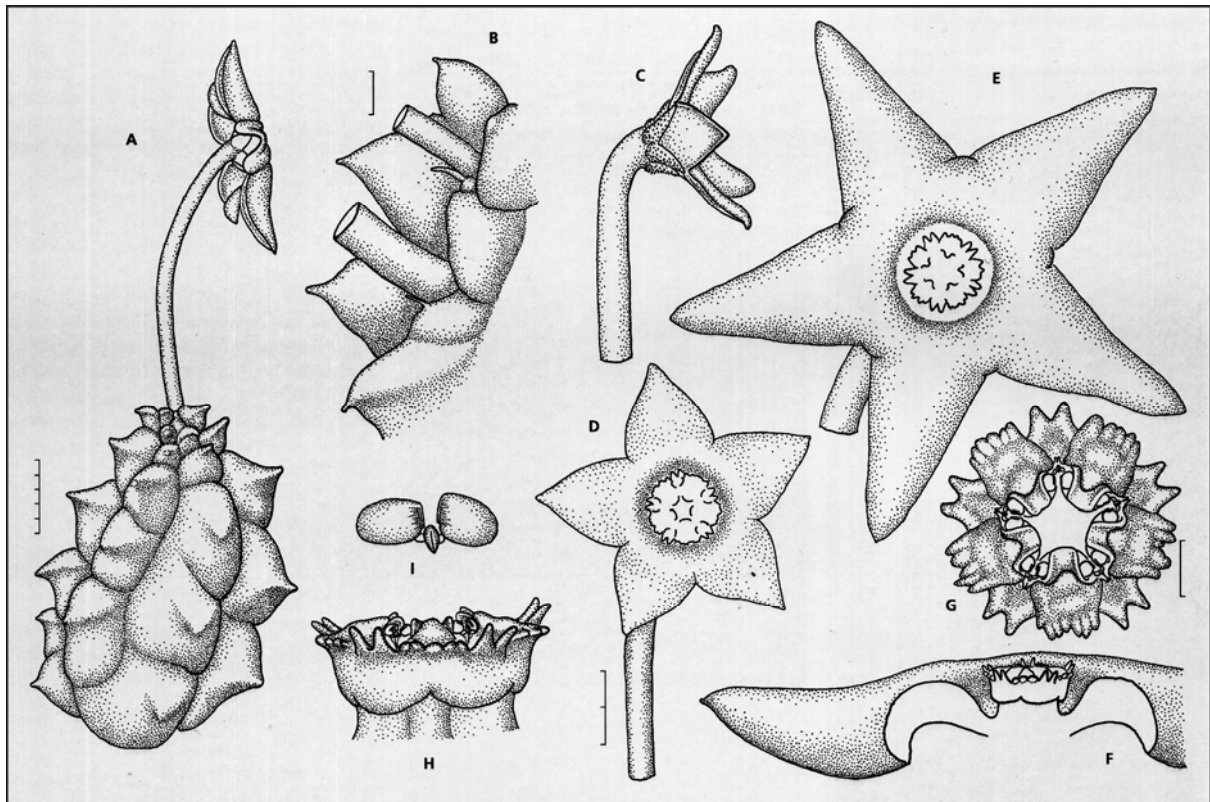


Fig. 11.22. *Pectinaria longipes* subsp. *longipes*. A, young stem with flower. B, inflorescences. C, side view of flower (less than half of pedicel shown). D, E, face view of flower. F, side view of dissected flower. G, face view of gynostegium. H, side view of gynostegium. I, pollinarium. Scale bars: A, 5 mm; B, F, 1 mm (at B); C, 3 mm (at A); D, E, 2 mm (at D); G, H, 0.5 mm (at G); I, 0.25 mm (at D). Drawn from PVB 982, north-west of Sutherland (no specimen).



Fig. 11.23. *P. longipes* subsp. *longipes*, Theron, Tierhoek, south-west of Fraserburg, showing the long pedicels.



Fig. 11.24. *P. longipes* subsp. *longipes*, Theron, Tierhoek, south-west of Fraserburg, with yellow corona.



Fig. 11.25. *P. longipes* subsp. *longipes*, PVB 2545, north-west of Sutherland, with reddish corona.

2b. *Pectinaria longipes* subsp. *villetii*

Pectinaria longipes subsp. *villetii* (C.A.Lückh.)

Bruyns, comb. et stat. nov.

Caralluma longipes vat. *villetii* C.A.Lückh., 'S.A.G.'

28: 228 (1938).

Type: Cape, near Loeriesfontein, Villets sub Lückhoff 263 (missing).

Lectotype (selected here): painting by CT. Villett (BOL).

Pedicel 4-25 mm long, holding flower facing upwards.
Corolla 6-8 mm diam.; **lobes** 2.5-4.0 mm long, 1.5 mm broad at base, broadly ovate-deltate, pale yellow to pale pink, margins slightly folded back.

Distribution and habitat

Subsp. *villetii* is only known around Loeriesfontein, in an area which is some 40 km north of the nearest collection of *P. maughanii* and 150 km north of the nearest locality for subsp. *longipes*.

In the area where it was rediscovered in 1999, plants were found in flattish or very gently sloping areas with few stones. Here they grew in areas dominated by small shrubs of *Ruschia spinosa*, which, mostly, were no more than 150 mm tall, though they spread outwards and may be up to 1 m in diameter. Specimens of subsp. *villetii* and several other stapeliads, including *Duvalia caespitosa*, *Orbea ciliata*, *Piarranthus punctatus*, *Quaqua acutiloba*, *Q. marlothii* and *Stapeliopsis exasperata*, grew in loose, humus-rich ground under these small shrublets.

Diagnostic features and relationships

As is to be expected, subsp. *villetii* is more variable than was given in the protologue and in the population recently encountered the pedicels were 9-25 mm long, whereas they were originally given as 4-6 mm long. However, the flowers generally seem to be very small and, at 6-8 mm in diameter, are often even smaller than in subsp. *longipes*. The main difference



Fig. 11.26. Charles T. de Mornet Villett packing collections of plants for transport back to Cape Town, probably in the 1930s (courtesy Cynthia Villett).

PECTINARIA MAUGHANII

between the two subspecies is that the corolla faces upwards in subsp. *villetii* and horizontally in the other.

Lückhoff mentioned that the tips of the corolla lobes could be deeper yellow than the rest or even rose-red. Among plants collected recently, some had pale pink flowers. The corolla lobes are slightly folded back so that the upper surface is convex.

History

Subsp. *villetii* was found a little before 1938 near Loeriesfontein by Charles T. Villet. It is not known exactly where he obtained material and on his painting in the Bolus Herbarium he has written, probably erroneously, that it hailed from Nieuwoudville. In September 1999 it was



Fig. 11.28. *P. longipes* subsp. *villetii*, PVB 7950, north-east of Loeriesfontein.



Fig. 11.27. *P. longipes* subsp. *villetii*, PVB 7950, north-east of Loeriesfontein.

recollected about 10 km east of Loeriesfontein and over 20 plants were seen in full flower. The tiny, pale yellow flowers left no doubt at all as to their identity.



Fig. 11.29. *P. longipes* subsp. *villetii*, PVB 7950, north-east of Loeriesfontein.

3. *Pectinaria maughanii*

Pectinaria maughanii (R.A.Dyer) Bruyns, *Cact. Succ. J. Gr. Brit.* 43:69 (1981).

Caralluma maughanii R.A.Dyer, *Rec. Alb. Mus.* 4:115

(1931). *Vadulia maughanii* (R.A.Dyer) Plowes, *Excelsa* 20:19 (2003).

Type: South Africa, Cape, near Nieuwoudtville, fl. Jan. 1929, Maughan-Brown 20 (GRA).

Stems 10-80 mm long, 10-15 mm thick, usually decumbent, occasionally prostrate, green to brownish green sometimes faintly mottled with purple; **tubercles** 2-4 mm long, tapering to acute and occasionally hard tooth.

Pedice 3-25 mm long, $\pm$ 0.75 mm thick, ascending to erect and holding flower facing upwards, often slightly fluted towards apex; **sepals** 1.5-2.0 mm long, $\pm$ 0.5 mm broad at base, lanceolate, acute, often with a few papillae dorsally near base. **Corolla** 10-17 mm diam., $\pm$ rotate; outside brownish green, smooth; inside deep yellow with pink to maroon on base of lobes and mouth of tube, with tube pale yellow, smooth; **tube** $\pm$ 0.5 mm long, broad and shallow and containing lower half of gynostegium; **lobes** 5-7 mm long, 2-3 mm broad at base, ascending to spreading, narrowly ovate-deltate, slightly broader at base then narrowing gradually to broadly acute tip, convex above from margins strongly folded back and usually nearly touching one other underneath. **Corona** $\pm$ 1.5 mm tall, 2.5 mm broad, dark purple-black, raised on very short stipe; **outer lobes** 1 mm long, erect, bifid to below middle into slender diverging terete to slightly flattened lobules, with pectinate portion behind inner lobes divided into 3 or more spreading terete obtuse lobules nearly reaching same height as outer lobes (lobules rarely absent); **inner lobes** $\pm$ 0.5 mm long, covering anthers and often meeting in centre, deltoid, emarginate.

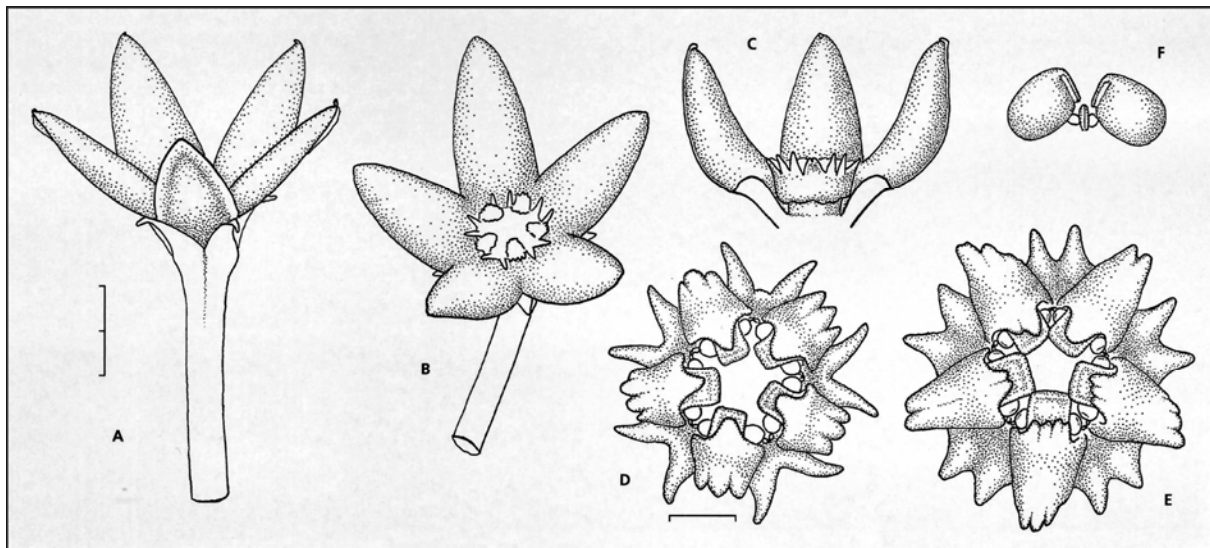


Fig. 11.30. *Pectinaria longipes* subsp. *villetii*. A, side view of flower. B, oblique view of flower. C, side view of dissected flower. D, E, face view of gynostegium. F, pollinarium. Scale bars: A-C, 2 mm (at A); D, E, 0.5 mm (at D); F, 0.25 mm (at A). Drawn from PVB 7950, north-east of Loeriesfontein.

Distribution and habitat

As far as is known, *P. maughanii* is restricted to the single latitude-longitude square 3119. Here it is quite plentiful in the relatively flat area between Calvinia, Nieuwoudtville and



Fig. 11.31. Herbert Maughan-Brown, c. 1935 (courtesy Roy Maughan-Brown).

near Grasberg in the north-west. It is almost exclusive to this flat area and only one collection {PVB 4319} has been made in the lower areas along the Hantam River to the north of this plateau.

Plants form clumps under small shrublets of *Eriocephalus* or *Ruschia spinosa* in slightly gravelly to loamy ground and can be very common. They seem to occur regularly together with *Quaqua aurea*.

Diagnostic features and relationships

This species with its attractive, deep yellow and maroon, bicoloured flowers is easily recognisable. The stems are often more erect than in any other *Pectinaria*, but they may also be prostrate with an only slightly upturned apex. The tubercles are tipped by a tooth which may become quite hard and covered with a horny, yellow-brown layer (and beginning to resemble somewhat those in *Quaqua*).

As in *P. longipes*, the flowers are held erect on a slender pedicel of extremely variable length but in *P. maughanii* they face upwards as well. The margins of the corolla lobes are recurved, so the upper surface is distinctly convex. This is already visible in the bud, in which the lobes are noticeably depressed along their middle.

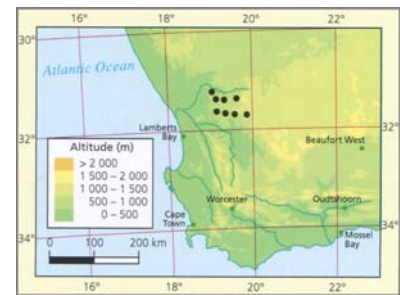


Fig. 11.32. Distribution of *Pectinaria maughanii*.

In *P. maughanii* the corona is generally dark purple-black and the teeth around the edge are fewer and longer than in any other *Pectinaria*. A few plants have been seen where the lobules of the dorsal projections of the inner lobes are entirely missing, but this is exceptional. The comparatively massive inner corona lobes have always been found to hide the anthers completely.

History

Pectinaria maughanii was discovered by Herbert Maughan-Brown (8 January 1883-5 February 1940) in September 1928 near Nieuwoudtville. Maughan-Brown was educated in England,

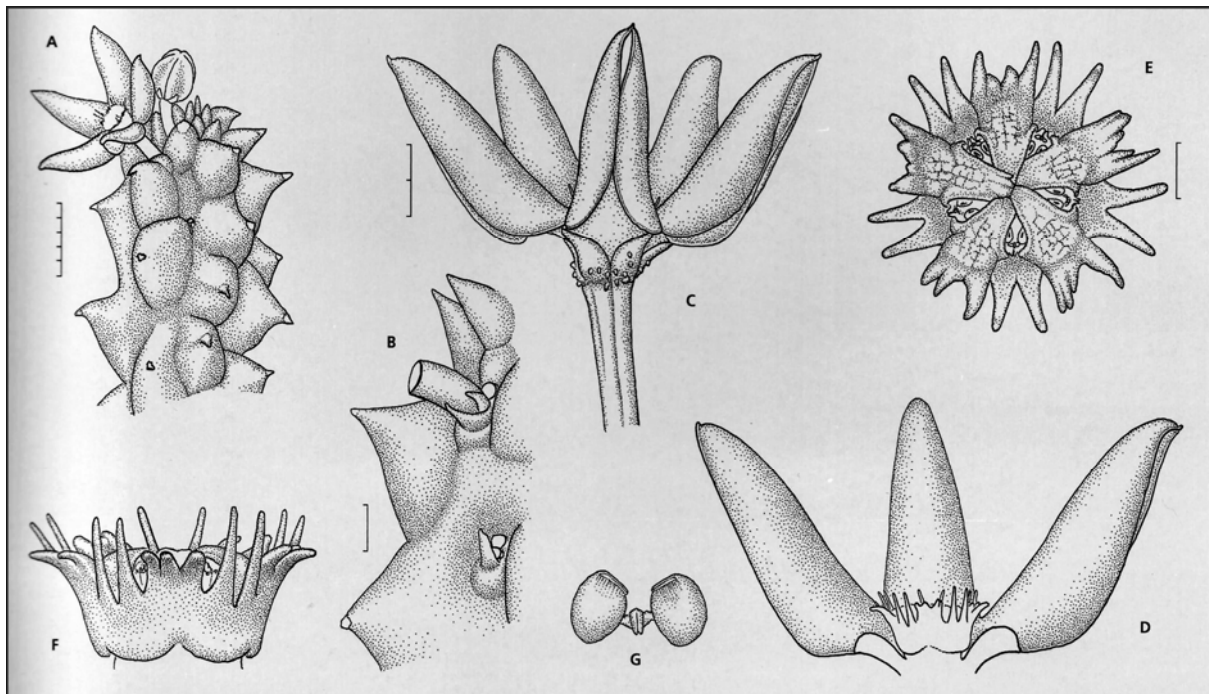


Fig 11.33. *P. pectinaria maughanii*. A, apex of stem with flowers. B, inflorescences. C, side view of flower. D, side view of dissected flower. E, face view of gynostegium. F, side view of gynostegium. G, pollinarium. Scales: A, 5 mm; B, D, 1 mm (at B); C, 2 mm; E, F, 0.5 mm; G, 0.25 mm (at C). Drawn from PVB 4308, north-west of Calvinia.

PECTINARIA MAUGHANII



Fig. 11.34. *P. maughanii*, PVB 6302, south-west of Calvinia. As this series of pictures shows, the flowers are very variable in colour.

where he studied medicine at Edinburgh University and obtained an M.D. in 1907. In 1919 he was appointed Chief Medical Inspector of Schools for the Cape Province and he held this position from 1920 till his death in 1940. Although he gave lectures in School Hygiene at the University of Cape Town, it is his considerable interest in natural history for which he is best remembered. During his visits to schools in outlying areas in the course of his duties, he discovered several unusual and previously unknown plants, many of which were succulents (Roy Maughan-Brown, pers. comm. 1999). Of his discoveries, *Conophytum maughanii*, *Dorotheanthus maughanii*, *Haworthia truncata* var. *maughanii*, *Pectinaria maughanii*, *Polyxena maughanii* and the monotypic *Maughaniella* (now regarded as a synonym of *Diplosoma*) are the best-known examples.



Fig. 11.35. *P. maughanii*, PVB 4308, north-west of Calvinia, with exceptionally short pedicels.



Fig. 11.36. *P. maughanii*, PVB 6302, south-west of Calvinia.



Fig. 11.37. *P. maughanii*, PVB 6302, south-west of Calvinia..



Fig. 11.38. *P. maughanii*, PVB 6302, south-west of Calvinia.

12. Piaranthus



Piaranthus was created by Robert Brown in 1810 for two species of *Stapelia* described by Masson, *S. pulla* and *S. punctata*. He defined this new genus by 'corona simple, 5-lobed, with the lobules toothed on the back'. Probably because of the confusion caused by R. Brown's inclusion of these two species

in a single genus, Haworth (1812) described a further genus, *Obesia*, in which he placed Masson's *Stapelia punctata*, *S. decora* and *S. geminata*. Later these names were moved to various other genera, including *Podanthes* and *Caralluma*. N.E. Brown (1878) found, apparently for the first time, that *S. pulla* did not fit the definition of *Piaranthus* at all. He discovered that the gynostegium had both inner and outer coronas so it had quite different affinities and was, in fact, a synonym of *Stapelia mammillaris* (now *Quaqua mammillaris*). Consequently he removed it from *Piaranthus* and moved *S. decora* and *S. geminata* into *Piaranthus* alongside *P. punctatus*. In so doing, he gave *Piaranthus* the character that we know today. Consequently *P. punctatus* (Masson) Schult. is taken as the type of the genus. After this, the number of species increased substantially, and in their account White & Sloane (1937) discussed 16 species. The first time that this unsatisfactorily large number of species was given attention was in the account by Bayer (1976). He considered that the clearly recognisable taxa were practically

restricted to their own geographical areas, though he mentioned that 'there are several anomalies on the borders of these areas which may present insoluble problems'. He therefore sought to define species according to consistencies in (1) outward appearance and in (2) occurrence in the field and distribution. On the basis of these criteria he deduced that there were seven species of *Piaranthus*. Meve (1994) revised *Piaranthus* as part of his doctoral thesis and in this account he also recognised seven species, of which one was new.

Also included in the present concept of *Piaranthus* is *Huerniopsis*. This genus was described by N.E. Brown for the single species *H. decipiens* (Brown 1878). He considered this to be most closely allied to *Huernia* but distinguished from *Huernia* by the 'utter absence of an outer corona'. Brown mentioned that, in this respect, his species resembled *Piaranthus* but that it had a different habit and a different corolla, and lacked dorsal crests on the corona. Curiously enough, in 1890 he described *Piaranthus grivanus* which was found to be a synonym

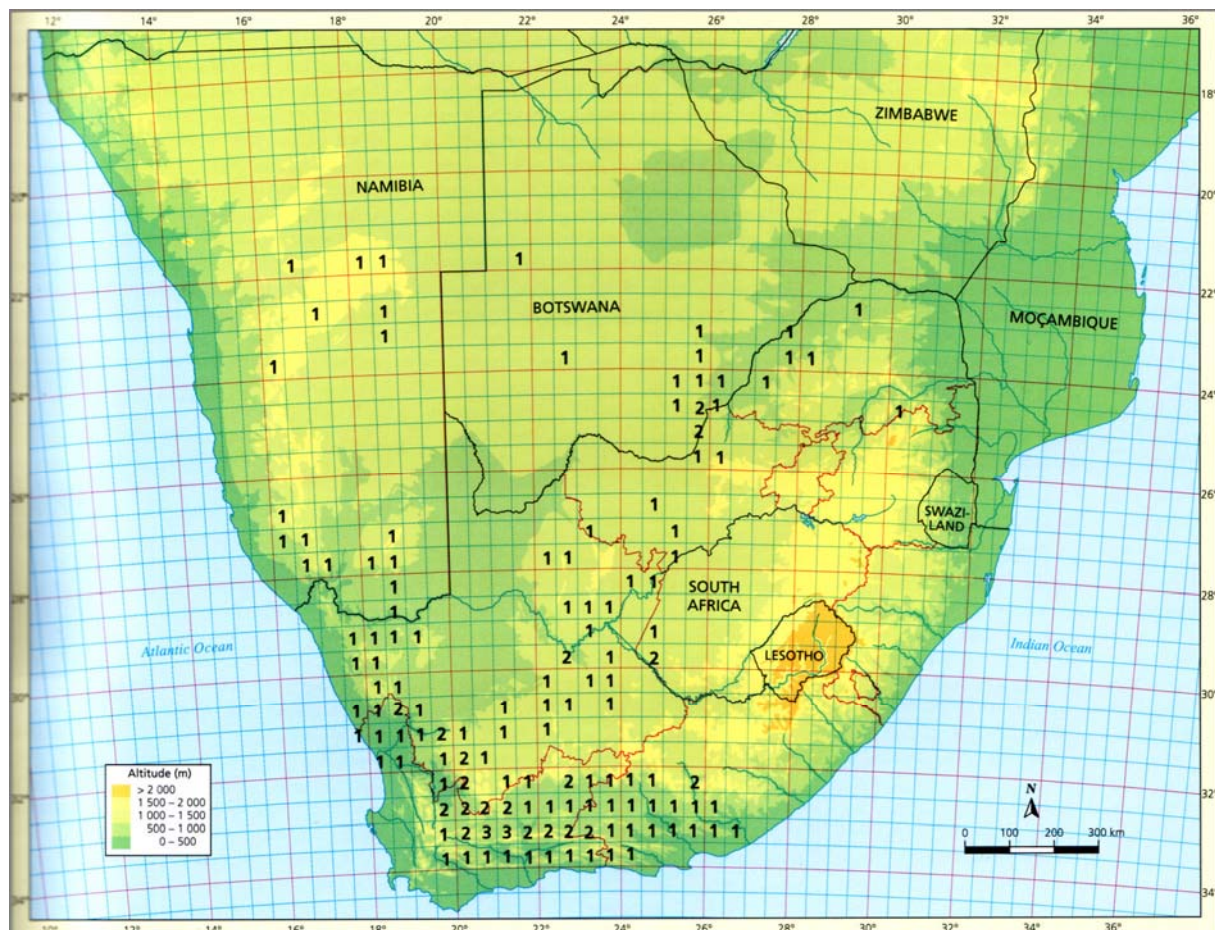


Fig 12.1. Patterns of diversity in *Piaranthus*, showing the number of species recorded to date in each half-degree square.

PIARANTHUS

of *Huerniopsis decipiens* (Bayer 1976), so he does not seem to have been very certain how to distinguish the two genera.

White & Sloane (1937) transferred a second species to *Huerniopsis* which had been described by N.E. Brown as *Stapelia atrosanguinea*. They, too, briefly mentioned the 'absence of an outer corona' shared between these two species and *Piarranthus*, but they did not otherwise explore the relationship between them. Meve (1994) also drew attention to the close relationship between *Piarranthus* and *Huerniopsis*, especially in the light of the apparent absence in both genera of an outer corona.

The relationship between these genera was investigated in more detail in Bruyns (1999b) after it was noticed that characters to separate the two genera could not be found. These investigations included studies of the ontogeny of the respective coronas which showed that, contrary to most published opinions, in both genera there were indeed two series of corona lobes but that the outer series was much reduced and often provided the crests behind the inner lobes. A cladistic treatment also showed that *Piarranthus* was nested within *Huerniopsis* and, therefore, that *Huerniopsis* was not monophyletic. Recent molecular investigations have revealed the same relationships (Meve & Liede 2002) and our own investigations show that there is strong statistical support for the inclusion of the two species of *Huerniopsis* in *Piarranthus*.

Piarranthus R.Br., *Asclepiadeae*: 12 (1810).
Lectotype: *Piarranthus punctatus* (Masson) Schult.

Obesia Haw., *Syn. Pl. Succ.*: 42 (1812).

Stapelia [unranked] *Obesiae* Schult. in Roem. & Schult., *Syst. Veg.*: 6: 42 (1820).

Stapelia sect. *Obesia* (Haw.) Decne. in DC, *Prodr.*: 8: 661 (1844).

Lectotype: *Obesia geminata* (Masson) Haw. [= *Piarranthus geminatus* (Masson) N.E.Br.].

Huerniopsis N.E.Br., *J. Linn. Soc. Bot.*: 17:171 (1878).

Type: *Huerniopsis decipiens* N.E.Br. [= *Piarranthus decipiens* (N.E.Br.) Bruyns].

Dwarf spineless non-rhizomatous succulent forming mats up to 300 mm (-1 m) diam. **Stems** 10-150 mm long, 5-20 mm thick, decumbent, somewhat clavate to ± globose, fleshy and firm, glabrous, green to grey-green or reddish, sometimes flecked with purple, finely papillate to smooth; **tubercles** 1-6 (-8) mm long, obscure and obtuse, not laterally flattened, joined into 4-5 rounded obtuse angles along stem, each tipped by small deltoid tooth 0.5-6.0 mm long subtended by 2 ± spherical stipular denticles. **Inflorescences** glabrous, 1-3 per stem, arising mainly towards apex of stem, each bearing 1-5 (-10) flowers often opening in rapid succession (often several open at once) on gradually lengthening knobbly peduncle 2-15 mm long with several lanceolate bracts 1-3 mm long often with small lateral teeth; **pedicel** 2-25 mm long, 1-2 mm thick, erect to ascending and holding flower fac-

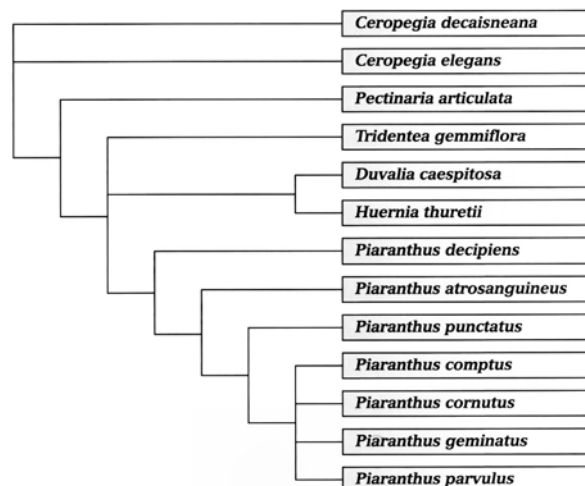


Fig. 12.2. Simplified cladogram derived from morphological characters showing the possible relationships among the species of *Piarranthus* (Bruyns 1996b).

ing upwards; **sepals** 1-9 mm long, 1-2 mm broad at base, lanceolate, acute to acuminate. **Corolla** 6-45 mm diam., rotate to campanulate, deeply lobed; outside glabrous and smooth, pale green often lightly spotted with purplish; inside covered with acute to ± spherical papillae, deep maroon to cream often dotted mottled or transversely striped with darker colour; **tube** up to 4-7 mm long, 5-10 mm broad at mouth, nearly absent to cupular, **corolla** scarcely to considerably thickened around mouth; **lobes** 5-18 mm long, (1.8-) 2-12 mm broad at base, spreading, lanceolate to narrowly ovate, acute, convex above with margins somewhat recurved, margins rarely with clavate cilia. **Corona** 2-13 mm tall, 2-7 mm broad, consisting of 2 series arising on staminal tube and partly intergrown (outer series very much reduced), glabrous, brown to yellow sometimes spotted with red, narrowing towards base and ± without basal stipe; **outer lobes** much reduced to rounded spreading ridge beneath guide-rail, often with broad ascending to spreading tuberculate-rugulose crest behind each inner lobe, with flap of tissue rising towards base of guide-rail and partly closing off nectarial cavity; **inner lobes** 1-10 mm long (sometimes absent in *P. punctatus* var. *framesii*), adpressed to backs of anthers at least in lower half of anthers, sometimes erect above and occasionally recurved towards tips, dorsiventrally flattened, lanceolate to ovate-lanceolate, ± acute, without dorsal projections. **Anthers** horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** ellipsoidal, insertion-crest twisting from outer edge onto dorsal surface, caudicle attached with broad cupular pad to base. **Follicles** erect, terete-fusiform, obclavate, slender, 30-140 mm long, 3-8 mm thick, consisting of 2 horns diverging at 30-60°, longitudinally mottled with purple, glabrous, smooth.

Plants in *Piarranthus* form diffuse to dense mats which may be anything between 100 and 500 mm in diameter (more rarely up to 1 m across). The stems are generally small, short (usually between one and three times as long as thick)

and decumbent, with most of the stem prostrate and only the apex erect or at least facing upwards. The tubercles along the stem are arranged into four or five blunt angles (in some cases these are so obscure that the stems are more or less spherical) and each of them is tipped with a small leaf-rudiment which wears off with time. The surface of the stem is smooth in most species but somewhat papillate (slightly sand-papery) in *P. atrosanguineus*, *P. cornutus* and in some forms of *P. geminatus*.

In *Piarranthus* there is mostly only a single inflorescence per stem and it matures above the middle of the stem, bearing 1-3 flowers, which often open in quick succession. In all species the flowers face upwards on more or less erect and comparatively (sometimes very) short pedicels.

Flowers in *Piarranthus* are small to medium in size and mostly between 15 and 35 mm in diameter (smallest in *P. parvulus* and largest in *P. atrosanguineus*). In *P. atrosanguineus* and *P. decipiens* they are unusually short-lived whereas in the other species they remain open for 2-4 days. Colours inside the flowers vary from deep maroon in *P. atrosanguineus* to white or yellow, often with transverse darker markings in the other species. The dark-flowered species emit a faint to strong, excrement-like odour but the paler-flowered ones have a variety of odours. Some are excrement-like but others are similar to decaying fruit or even rather like honey. Several species have more or less no corolla tube (*P. comptus*, *P. cornutus*, *P. geminatus* and *P. parvulus*) but in *P. punctatus*, *P. decipiens* and *P. atrosanguineus* there is a significant and often prominently pentagonal tube in the centre of the flower in which the gynostegium is situated. The corolla is slightly to noticeably thickened around the mouth of this tube, with

this thickening often concentrated beneath the sinuses of the lobes. The corolla lobes spread and are somewhat convex above from the slightly reflexed margins. In a few cases they are adorned with vibratile, clavate cilia. The inside of the corolla is generally covered with fine, spike-like papillae (these have an unusual, almost spherical shape in some plants of *P. punctatus*, fig. 27 B) and may, on a larger scale, also be somewhat rugulose.

The corona in *Piaranthus* is distinctive among southern African stapeliads for the lack of a basal stipe and for the very much reduced outer series. The spreading portion of the outer corona which is normally found between the anthers and below the guide-rails is progressively lost (it is longest in *P. decipiens*, shorter in *P. atrosanguineus* and almost absent in the remaining species). It is progressively replaced by a vertical lip which points towards the base of the guide-rail and encloses an increasingly deep nectarial cavity below the guide-rails (the area marked 'N' in fig. 30, C-F). In most species formerly placed in *Piaranthus* the inner lobes are dorsiventrally fattened and at least partly adpressed to the backs of the anthers. Behind each of them there is a conspicuous, tuberculate crest which has generally been referred to as the dorsal projection or dorsal crest of the inner lobes (White & Sloane 1937; Meve 1994). However, studies of its development (Bruyns 1999b) revealed that it is actually part of the outer series: it was found that adjacent outer lobes each contribute to it and the zone of fusion of these two parts is actually visible for quite a while during its development and can sometimes be made out in the adult corona

too. The extraordinary coronal structure of '*P. framesii*', where this 'dorsal crest' is absent and where the inner corona lobes may also be absent, is discussed in detail under *P. punctatus*.

The pollinaria are very similar across the genus. They are unusually large in *P. atrosanguineus* and *P. decipiens* (fig. 32 E), where they also have particularly large corpuscles, but in the other species there is much variation and in some cases they approach these in size. The pollinia are always longer than broad, ellipsoidal in shape and have the insertion-crest twisting up onto the dorsal surface.

The first two species recognised here are widely distributed over the central summer-rainfall parts of southern Africa in southern and eastern Botswana, central Namibia and central South Africa. The remaining species are found further to the south-west, in southern Namibia, the Western Cape, the Eastern Cape and in the western corner of the Free State. The genus as a whole therefore has a wide and somewhat diffuse distribution across southern Africa, with the main body of records from along and east of the boundary of the winter-rainfall area in the south-western corner of the subcontinent (fig. 12.1).

Over most of the area where *Piaranthus* is found there is only one species per half-degree square. A few exceptions occur. Examples of these are where *P. atrosanguineus* and *P. decipiens* grow near one another in Botswana, where *P. decipiens* and *P. cornutus* occur near one another along the Orange River near Kimberley, and where *P. cornutus* meets up with the more local species towards the west.

A maximum of three species is found where *P. comptus*, *P. geminatus* and *P. parvulus* grow near one another between Matjiesfontein and Laingsburg.

Species of *Piaranthus* are almost always found sheltering under bushes. These vary from *Grewia* and small specimens of *Acacia* in the summer-rainfall areas to shrublets of the *doringvygies* *Ruschia spinosa* and *R. divaricata* or other small, often non-succulent bushlets such as species of *Pteronia* (especially *P. pallens*, *P. glomerata* and *P. incana*) nearer the winter-rainfall area.

It has been found over the past 10 years that the distribution of *Piaranthus* s. str. was not as well known as was thought and many new records have been made during this period. These have also shed light on the 'anomalies' referred to by Bayer (1976) and enabled the hypotheses proposed by Meve (1994) to be tested.

According to Meve (1994), the species of *Piaranthus* form 'a complex of extremely nearly related species. This impression is intensified by the occurrence of many lines of transition within or between the species which sometimes make it difficult to decide where a single specimen has to be placed' (p. 66). He added that 'interlaced with numerous transitions, it is nearly impossible to present a short and precise key. Single specimens of one taxon not rarely show features typical for another species' (p. 68). In this treatment he recognised seven species, though it is not clear how these were delimited in view of the extensive intergradation that he had found in his investigations.

If one examines the data that he provided, it is clear that *P. punctatus* and *P. framesii* are

Key to the species

1. Corolla with distinct tube2.
2. Corolla inside white to pale yellow spotted to transversely banded with red to purple, corona yellow, part of outer corona lobe beneath guide-rails absent3. *P. punctatus*
2. Corolla inside deep maroon to brown or brown-red (rarely with some transverse stripes), corona often purple to pink or brown (sometimes cream), part of outer corona lobe beneath guide-rails present3.
3. Corolla 20–30 mm diam., corona purple, pink or pale brown, outer lobes forming shallow pouch joining 'bases' of inner lobes, inner lobes 3–6 mm long1. *P. decipiens*
3. Corolla 40–45 mm diam., corona pale orange-yellow becoming cream to white on inner lobes, outer lobes divided into 2 short truncate flaps often somewhat pressed together, inner lobes 8–10 mm long2. *P. atrosanguineus*
1. Corolla without distinct tube4.
4. Corolla 6–13 mm diam., corolla lobes mostly less than 2.2 mm wide7. *P. parvulus*
4. Corolla 14–42 mm diam., lobes at least 3 mm wide5.
5. Corolla inside white to cream with bold red or red-brown spots (rarely transversely banded with red to red-brown), corolla 14–17 mm diam6. *P. comptus*
5. Corolla inside white to pale brown without darker markings or, if marked, then with irregular transverse lines often coalescing in dark patch at tips of lobes, corolla mostly larger than 20 mm diam6.
6. Stems somewhat papillate7.
7. Inner corona lobes ascending beyond middle of anthers5. *P. cornutus*
7. Inner corona lobes adpressed to backs of anthers and not ascending beyond middle8.
8. Plants from Namibia5. *P. cornutus*
8. Plants from Western or Eastern Cape4. *P. geminatus*
6. Stems not papillate4. *P. geminatus*

PIARANTHUS DECIPIENS

separated from all the others by the presence of a corolla tube that contains the gynostegium and by their relatively tall gynostegium from its base to the level of the anthers: if one ignores the sometimes erect inner lobes (in *P. parvulus* and *P. cornutus*), the gynostegium in the others is broader than tall while in *P. punctatus* and *P. framesii* it is at least as tall as broad. However, there are problems with the recognition of even these two species. The presence of intermediates between the two was first discussed by Bayer & Plowes (1975a) and my own collecting has revealed more of these populations with intermediates.

Actually, despite the relatively obvious differences in the shape of the corolla, the separation of *P. punctatus* and *P. cornutus* is not as clear-cut as has been made out. This is discussed under *P. punctatus*.

P. parvulus is readily separable from all the others by its small flowers (6-13 mm diam.) in which the corolla lobes are less than 2.2 mm wide. This separation is further apparent from its relative infertility with the other taxa with which it occurs (Meve 1994: 66) and this is largely brought about by a physical barrier caused by the small size of the pollinia.

The remaining four species that were recognised are very difficult indeed to separate. Meve's Table 4 shows that characters are entirely mixed across the species *P. barrydalensis*, *P. comptus*, *P. decorus* and *P. geminatus* and they are impossible to separate reliably. My own collecting has not shown that *P. barrydalensis* occurs together with *P. geminatus* (as Meve claimed) but rather that it is not separated by any discontinuities from the western forms of *P. geminatus* that Meve called '*P. geminatus* forma *disparilis*'. This species is therefore synonymous with *P. geminatus*. Recent collecting has also revealed two widely separated localities at which '*P. decorus* subsp. *decorus*' and 'subsp. *cornutus*' grow together, without any sign of intergradation. Meve mentioned '*decorus*-like' individuals amongst populations of 'subsp. *cornutus*' but his evidence for this turns out to be confused and no new evidence has been located. Consequently the data available point to 'subsp. *cornutus*' being a separate species from 'subsp. *decorus*' and this is how it is treated here. 'Subsp. *decorus*' is considered to be part of the '*P. geminatus*' complex.

The relationships between *P. cornutus* and *P. comptus* and between *P. comptus* and *P. geminatus* are still not adequately understood. The differences between *P. comptus* and *P. geminatus* are small, there is some evidence of intermediates and they are not known to occur together (though they occur within one half-degree square). In addition, as Meve (1994: Table 3) found, *P. comptus* turns out to be readily crossable with *P. decorus* and *P. geminatus*. Nevertheless, for the time being, *P. comptus* is maintained as a distinct species.

1. *Piaranthus decipiens*

Piaranthus decipiens (N.E.Br.) Bruyns, Syst. Bot. 24: 396 (1999).

Huerniopsis decipiens N.E.Br., J. Linn. Soc. Bot. 17: 171 (1878).

Type: South Africa, Cape, MacOwan 2246 (K).

Piaranthus grivanus N.E.Br., Hooker's Icon. PL 20: t.1924 (1890).

Caralluma grivana (N.E.Br.) Schltr., J. Bot. 36: 479 (1898).

Type: South Africa, Griqualand West, Griva, Arnot sub Barkly 11 (K).

Stems 20-150 mm long, 8-20 mm thick, dull green to grey often mottled with purple; **tubercles** $\pm$ rectangular, laterally flattened, joined into 4 (very rarely 5) angles up stem, each bearing towards apex a narrowly deltoid leaf-rudiment 3-6 mm long with 2 stipular denticles at its base, leaf-rudiments soon drying out, often persisting as weak whitish spinescent husk. **Inflorescences** usually 1 per stem, arising in upper half, of 1-3 flowers developing in gradual succession, occasionally with small peduncle up to 5 mm long with several lanceolate laterally toothed bracts 1.5-3.0 mm long; **pedicel** 2-6 mm long, 2 mm thick, ascending, pinkish; **sepals** 6-8 mm long, $\pm$ 2 mm broad at base, lanceolate, acuminate, spreading to descending in upper half, pale grey-green. **Corolla** 20-30 mm diam., shallowly campanulate; outside spotted and longitudinally streaked with dull purple on grey-green; inside brown-red or brown becoming finely mottled with yellow in base of tube, sometimes conspicuously mottled with yellow all over, sometimes faintly transversely rugulose, with low rounded papillae each with a small apical bristle; **tube** 4-10 mm long, 7-10 mm broad at mouth, cupular, pentagonal, with **corolla** thickened around mouth beneath sinuses of lobes; **lobes** 7-12 mm long, 6-8 mm broad at base, deltate-ovate, acute, ascending to recurved, convex above with margins slightly recurved, with clavate purplish vibratile cilia 1.5-2.2 mm long along margins near bases. **Corona** 7-10 mm tall, 6-7 mm broad, seated on very

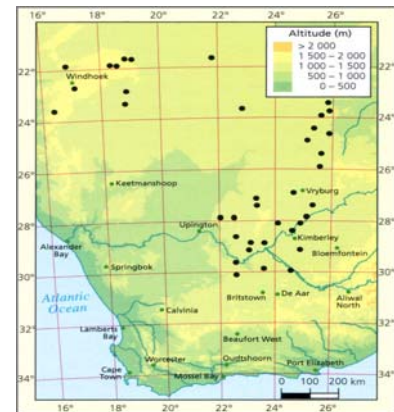


Fig. 12.3. Distribution of *Piaranthus decipiens*.

short stipe, purple to pink or pale brown, exterior usually with sweat-like droplets secreted over surface; **outer lobes** < 1 mm long, spreading, forming shallow pouch joining 'bases' of inner lobes; **inner lobes** 3-6 mm long, initially incumbent on backs of anthers then erect and connivent above them, dorsiventrally flattened and somewhat broadened below, $\pm$ terete and narrower above, parts above anthers very closely laterally adpressed to one another, acute to obtuse.

Distribution and habitat

Piaranthus decipiens occurs over a very wide area in Namibia, Botswana and South Africa, around the northern and eastern edges of the driest parts of the Kalahari. In Namibia it is found in the central area from Nauchas eastwards to Epukiro and Gobabis and southwards



Fig. 12.4. *P. decipiens*, PVB 6450, Kang Pan, Botswana, with speckled flowers.

towards Leonardville. It is widely and rather scantily recorded in Botswana. The area in Botswana around Ghanzi is particularly poorly collected and it is undoubtedly more plentiful than the two recent collections which have been made there indicate. It is rather better known in the south-east, where it is found from Lephephe southwards to Lobatse. It has been most frequently collected in South Africa from about 50 km south of Prieska northwards to the edge of the Kalahari and eastwards past Vryburg to Mafikeng and to around Schweizer-Reinecke.

Over this vast area *P. decipiens* is occasionally found at the foot of large shrubs or trees. More usually it grows in overgrazed situations under small bushes, which are often greatly reduced specimens of *Acacia tortilis* or, in some places around Schweizer-Reinecke, shrublets of *Ruschia spinosa*. Plants generally grow on firm, loamy ground and often on calcrete, but only rarely in sandy places.

Diagnostic features and relationships

Plants of *P. decipiens* form diffuse mats which are normally 150-300 mm across but may reach 1 m in diameter.



Fig. 12.5. *P. decipiens*, PVB 5476, near Gobabis, Namibia, specimen with unusually boldly mottled flowers.

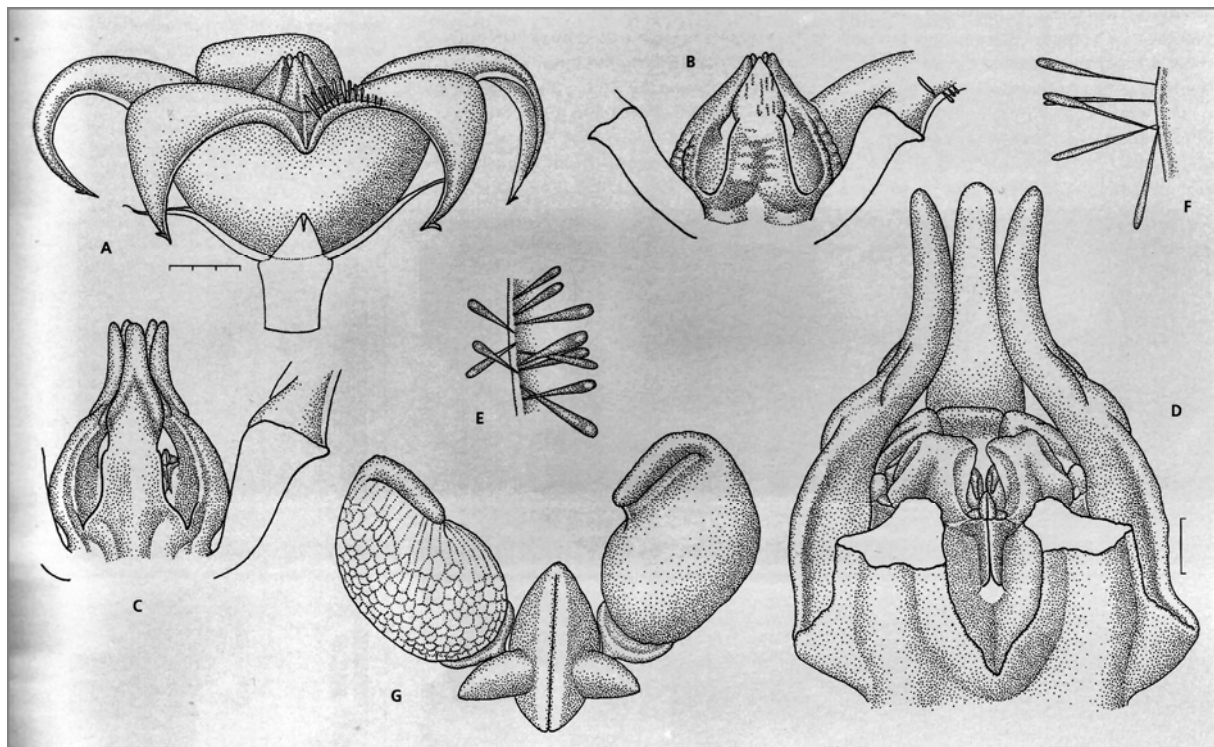


Fig. 12.6. *Piaranthus decipiens*. A, side view of flower. B, C, side view of centre of dissected flower. D, side view of gynostegium with two inner corona lobes removed. E, F, cilia on margins of lobes. G, pollinarium. Scale bars: A-C, 3 mm (at A); D-F, 1 mm (at D); G, 0.25 mm (at A). Drawn from: A, B, PVB 5634, Nauchas, south-west of Windhoek, Namibia; C, D, E, G, Bayer 1432, Thorn Park, Pitsani, Botswana; F, Leach 12497, Kathlahong (no specimen).

PIARANTHUS ATROSANGUINEUS

Although the stems are occasionally up to 150 mm long, they are mostly less than 50 mm tall and so are comparatively small, though typical for the genus. They are decumbent, often with a distinctly narrow base and this makes them fairly clavate in outline. The tubercles are mostly joined into four angles along the stems. Initially each is tipped with a small, narrowly deltoid leaf-rudiment with two quite obvious, though small, stipular denticles at its base. This leaf-rudiment rapidly dries out but persists for a while as a whitish husk and only gradually wears away.

Flowers are produced in small numbers towards the tips of the younger stems. In cultivation in Cape Town they have usually opened in the afternoon, remained open that night, the next day and night and then closed during the following morning. They therefore remain open for a total of about 40-42 hours and this corresponds exactly to the observations in this regard by N.E. Brown (1902-03: 500). They emit a faint odour of excrement.

In *P. decipiens* the flowers are at most 30 mm across, usually brown becoming paler in the tube and finely papillate-rugulose. Occasionally the whole flower is prettily mottled with yellow on brown. The lobes usually spread out and have a small patch of purplish vibratile cilia along the margins near the base. The mouth of the tube is conspicuously thickened to project inwards just below the sinuses of the lobes. This gives the tube a prominently pentagonal shape, where it is narrower behind the inner corona lobes and broader opposite the guide-rails.

The corona is almost contained in the tube and appears to consist mainly of the relatively large inner lobes with the outer lobes merely filling the space between them. Detailed studies of the development of these



Fig. 12.7. *P. decipiens*, PVB 6410, Boatlaname, Botswana, with particularly large and attractively marked flowers somewhat similar to the type of *Huerniopsis papillata* (but without the appropriate corona lobes).

corona lobes (Bruyns 1999b) has shown that the outer series contributes the lower part to these large, apparent 'inner lobes'. The small outer lobes conceal a relatively large nectarial cavity beneath the guide-rails which descends nearly to the base of the gynostegium (fig. 30 C, 34 D). The inner lobes are tightly adpressed to each other along their sides and rise in the centre to form a cone above the anthers. They usually have plenty of sweat-like droplets of nectar on their outer surface. These secretions were observed to be sweet first by N.E. Brown (1902-03: 500) but nothing is known about their chemical composition.

History

This species was described from material sent to N.E. Brown by Peter MacOwan in about 1875 from an unknown locality in the Cape Colony. Brown (1878) mentioned that he had already been cultivating it for several years before this, but there are no records from this material or information as to who had discovered it and sent it to him.



Fig. 12.8. *P. decipiens*, PVB 6450, Kang Pan, Botswana, from same place as fig. 12.4. Most flowers are uniformly coloured like this.

2. *Piaranthus atrosanguineus*

Piaranthus atrosanguineus (N.E.Br.) Bruyns, Syst. Bot. 24: 396 (1999).

Stapelia atrosanguinea N.E.Br., Gard. Chron. Ser. 3, 30: 425 (1901).

Caralluma atrosanguinea (N.E.Br.) N.E.Br., Fl. Trop. Afr. 4 (1): 485 (1903).

Huerniopsis atrosanguinea (N.E.Br.) A.C. White & B. Sloane, Stap., ed. 2, 3: 973 (1937).

Type: Botswana, north Kalahari, Jan. 1899, Lugard 263 (K).

Huerniopsis gibbosa Nel in A.C. White & B. Sloane, Stap., ed. 2, 3: 1174 (1937).

Type: Botswana, Lobatsi, Nel sub SUG 7358 (BOL).

Huerniopsis papillata Nel in A.C. White & B. Sloane, Stap., ed. 2, 3: 972 (1937).

Type: Botswana, Debeeti, Nel sub SUG 7347 (missing).

Lectotype (selected here): White & Sloane, Stap., ed. 2, 3: fig. 1041.

Stems 20-150 mm long, 8-20 mm thick, dull green to grey often mottled with purple; **tubercles** ± rectangular, laterally flattened, joined into 4 (very rarely 5) angles up stem, each bearing towards apex a narrowly deltoid leaf-rudiment 3-6 mm long with 2 stipular denticles at its base, leaf-rudiments soon drying out, often persisting as weak whitish spinescent husk. **Inflorescences** usually 1 per stem, arising in upper half, of 1-3 flowers developing in gradual succession, occasionally with small peduncle up to 5 mm long with several lanceolate laterally toothed bracts 1.5-3.0 mm long; **pedicel** 5-7 mm long, 2 mm thick, ascending, pinkish; **sepals** 6-9 mm long, 2 mm broad at base, lanceolate, acuminate, spreading in upper half, pale grey-green. **Corolla** 40-45 mm diam., rotate; outside glabrous, grey-green mottled with purple; inside deep maroon to brown sometimes becoming beige towards tips of lobes and rarely mottled with cream around

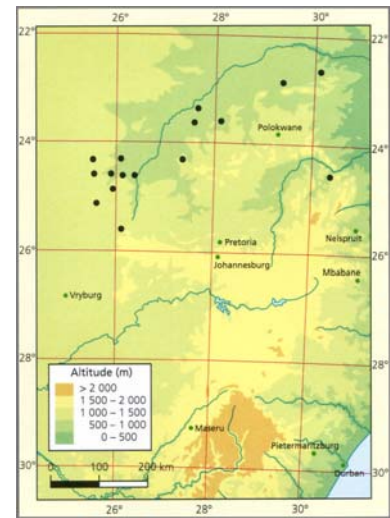


Fig. 12.9. Distribution of *Piaranthus atrosanguineus*.

mouth of tube, faintly transversely rugulose on lobes and finely papillate; **tube** 3-7 mm long, $\pm$ 8-10 mm broad at mouth, cupular, with **corolla** considerably thickened around mouth below sinuses of lobes, pentagonal; **lobes** 15-18 mm long, 9-12 mm broad at base, narrowly ovate, acute, spreading to slightly reflexed, convex above from slightly recurved margins, eciliate. **Corona** 10-13 mm tall (including inner lobes), 6-7 mm broad, $\pm$ without basal stipe, covered with sweat-like droplets of nectar on outer lobes and bases of inner lobes; **outer lobes** <2 mm long, divided into 2 short truncate sometimes somewhat papillate flaps often somewhat pressed together between inner lobes, pale orange-yellow; **inner lobes** 8-10 mm long, incumbent on backs of anthers then rising up and finally spreading to recurved, linear-terete to slightly laterally flattened and sometimes spirally twisted above, obtuse, pale orange-yellow below becoming cream to white (rarely pale brown) above.

Distribution and habitat

Piaranthus atrosanguineus is generally found to the east of *P. decipiens*, beginning around Gaborone and Molepolole in south-eastern Botswana and continuing into the north-western corner of the former Transvaal, where it is widely and scantily recorded from Zeerust northwards Ellissas and then into the area north of the Soutpansberg. There is also a record from the Burgersfort area much further east. The two species grow together around Gaborone and Molepolole but as yet no hybrids have been recorded.



Fig. 12.10. *P. atrosanguineus*, PVB 7777, near Nzehele Dam, north of the Soutpansberg, uniformly coloured flower with long inner corona lobes.

Piaranthus atrosanguineus has been seen in fairly tall *Acacia-Grewia* bush but on several occasions it has been collected among very small, heavily grazed bushlets of *Acacia tortilis* or under and next to spiky plants of *Euphorbia limpopoana*, which sometimes forms dense stands in overgrazed spots on shallow, stony ground.

Diagnostic features and relationships

Vegetatively identical, the two former species of *Huerniopsis* cannot be separated until just before the flowers open. The buds of *P. atrosanguineus* become quite a bit larger and have a distinctly narrower tube at the base, which becomes obvious shortly before the flower opens.

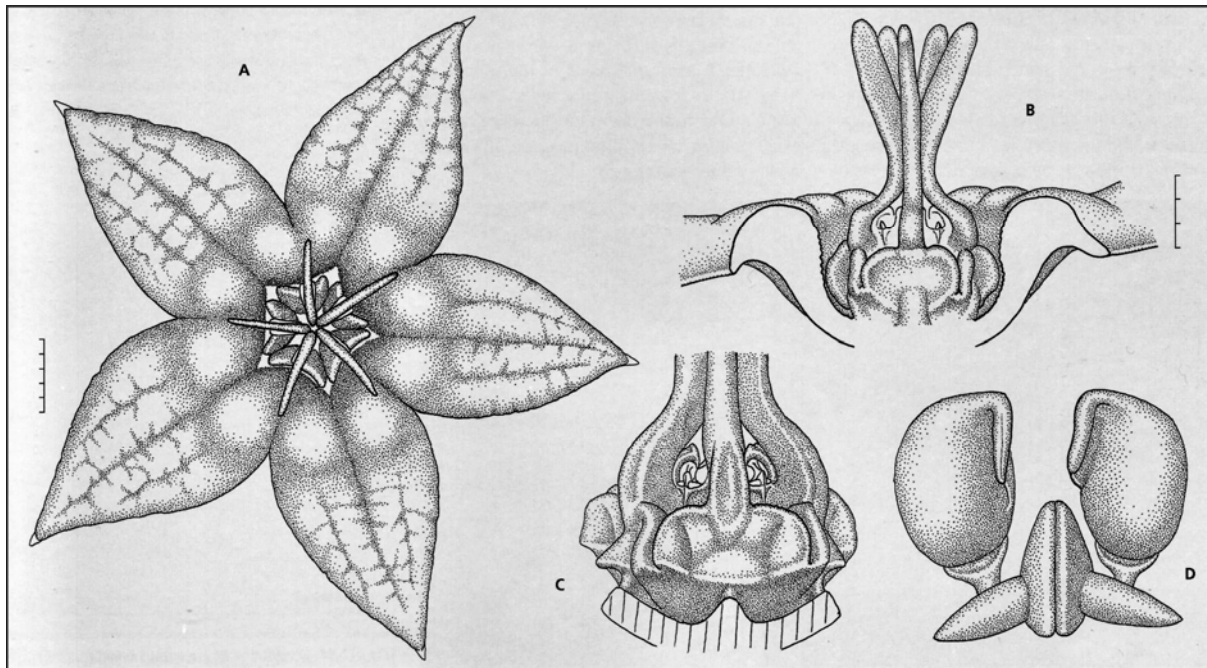


Fig. 12.11. *Piaranthus atrosanguineus*. A, face view of flower. B, side view of centre of dissected flower. C, side view of gynostegium. D, pollinarium. Scale bars: A, 5 mm; B, 3 mm; C, 2 mm (at B); D, 0.25 mm (at B). Drawn from: PVB 6538, near Matlabas.

PIARANTHUS PUNCTATUS

Flowers in *P. atrosanguineus* are the most short-lived amongst the stapeliads. In cultivation in Cape Town they have generally opened in the afternoon between 4 and 5 and closed again during the course of the following morning between 7 and 9, remaining open for a total of 18 hours or less. As usual, there are exceptions and one flower remained open for over 30 hours, although all others produced by the same plant lasted for the customary 16-18 hours. They have a strong, unpleasant odour that is emitted mainly during the first couple of hours that they are open.

At 40-45 mm across, the flowers here are markedly larger than those of *P. decipiens* and are the largest and most spectacular in *Piarranthus*. The lobes spread out or may sometimes be slightly reflexed, so the inside is nearly flat. Below the lobes there is a broad but shallow pentagonal tube in the centre. The mouth of this tube is much emphasised and slightly constricted by five inwardly spreading swellings below the sinuses of the lobes. As in *P. decipiens*, the exterior of the bud is boldly striped with purple. The inside of the corolla is a deep, rich and velvety maroon or brown that sometimes becomes paler towards the tips of the lobes. In some cases the lobes have a distinctly pale apical patch. The transverse mottling that is sometimes found in *P. decipiens* is very rare here.

The corona of *P. atrosanguineus* is more ornate than that of *P. decipiens*. The pale orange outer lobes are small and become covered with sweat-like drops of nectar. They consist of short, spreading structures which are often rather papillate on the margins and are raised up and sometimes even pressed together to form a narrow channel. The narrowness of this channel tends to hold nectar produced by the guide-rails in a pool around and below the rails by adhesion to the sides of



Fig. 12.12. *P. atrosanguineus*, PVB 6538, near Matlabas, corolla lobes paler than in next figure.

the channel. So much of this nectar is produced in this species that it has to be drained off if one wishes to gain access to the guide-rails to pollinate the flower. This excess nectar would presumably be consumed by insects that visit the flower and would not present a problem in nature. The relatively narrow inner lobes are addressed to the anthers and then rise above them in a column, afterwards diverging and sometimes spreading and even occasionally becoming spirally twisted. Towards the base they are pale orange like the outer lobes, but usually become whitish towards their tips. They are also covered with drops of nectar but mainly towards their bases.

History

Piaranthus atrosanguineus was discovered by Edward J. Lugard in Botswana in January 1899 and he brought a living specimen to Kew one month later, from which N.E. Brown was able to describe it. Lugard was said to have collected *P. atrosanguineus* in the 'northern Kalahari Desert', but it has never been seen again so far to the north-west and it is more likely that he collected it in eastern Botswana on the return journey.



Fig. 12.13. *P. atrosanguineus*, PVB 6402, near Modipane, Botswana, with slightly pale tips to the corolla lobes.

3. Piaranthus punctatus

Piaranthus punctatus (Masson) Schult. in Roem. & Schult., *Syst. Veg.* 6: 9 (1820).

Stapelia punctata Masson, *Stap. Nov.*: 18, t. 24 (1797).

Obesia punctata (Masson) Haw., *Syn. Pl. Succ.*: 43 (1812).

Caralluma punctata (Masson) Schltr., *J. Bot.* 36: 478 (1898).

Type: South Africa, Namaqualand, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 24.

Stems 10-60 (-100) mm long, 8-20 (-25) mm thick, occasionally $\pm$ clavate, green to purplish green, slightly papillate; **tubercles** with apical deltoid leaf-rudiment 0.5-2.0 mm long, bearing 2 minute stipular glands at base. **Pedicle** 5-20 mm long, 1.5-2.0 mm thick; **sepals** 2-4 mm long, 1 mm broad at base. **Corolla** 17-28 mm diam., campanulate; inside white to pale yellow spotted to transversely banded with red to purple, markings becoming smaller and fading towards base of tube, rarely uniformly pale yellow all over, covered with fine $\pm$ spherical to conical-acute papillae (< 0.2 mm long); **tube** 4-7 mm long, 5-9 mm broad at mouth, cupular, circular to pentagonal in outline, **corolla** not thickened towards mouth; **lobes** 6-13 mm long, 4-7 mm broad at base, spreading to somewhat reflexed, deltate, acute, with margins recurved except near base, rarely with few $\pm$ clavate cilia < 1 mm long near base. **Corona** 3.0-5.5 mm tall, 3.5-5.5 mm broad, yellow; **outer lobes** $\pm$ absent beneath guide-rails, forming rounded to deeply rugose-tuberculate crest ± 1 mm broad behind inner lobes to absent (in var. *framesii*); **inner lobes** 0.5-2.0 mm long, 0.5-1.0 mm broad (sometimes absent in var. *framesii*), addressed to backs of anthers to erect, usually exceeding anthers and sometimes ascending beyond them, narrowly deltoid to linear to oblanceolate, cune to truncate-emarginate, often dorsally channelled and with numerous ridges and **tubercles** towards rear and crest of outer lobes.

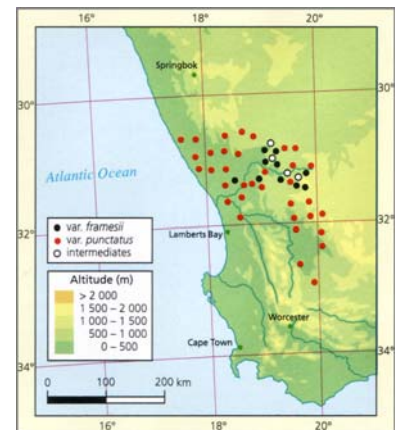


Fig. 12.14. Distribution of *Piaranthus punctatus*.

3a. *Piaranthus punctatus* var. *punctatus*

Corolla 17-28 mm diam.; inside covered with fine $\pm$ spherical to conical-acute papillae; **tube** usually not constricted towards mouth and circular at mouth; **lobes** rarely with few small marginal cilia. **Corona** 3.0-4.5 mm tall, 3.5-5.0 mm broad, $\pm$ circular when viewed from above, **outer lobes** forming rounded to deeply rugose-tuberculate crest $\pm$ 1 mm broad behind inner lobes; **inner lobes** 1-2 mm long, 0.5-1.0 mm broad, adpressed to backs of anthers, narrowly deltoid to oblanceolate, often channelled and ridged dorsally.

Distribution and habitat

Var. *punctatus* is found in Namaqualand mainly on the Knersvlakte and northwards to the Groen River near Garies. From here it extends eastwards to near Loeriesfontein and onto the higher areas around Calvinia and east of Nieuwoudtville. Further south it is also found on the Ceres Karoo, but it occurs rather sparsely along the western edge of this region

to about 30 km north-east of Karooport and also sporadically along the eastern side to between the foot of Gannaga Pass and the base of Ouberg Pass.

Specimens are frequently associated with various gregarious species of *Ruschia* (e.g. *R. spinosa* and *R. comptonii*) or *Pteronia* [*P. glomerata* and *P. ciliata*] and grow in flattish areas under these small shrubs, often becoming locally very common.

Key to the varieties of *P. punctatus*

- Corolla tube distinctly pentagonal at mouth, corona strongly pentagonal when viewed from above, inner corona lobes slender to absent **3b. var. *framesii***
 Corolla tube usually circular at mouth, corona $\pm$ circular when viewed from above, inner corona lobes deltoid to oblanceolate **3a. var. *punctatus***

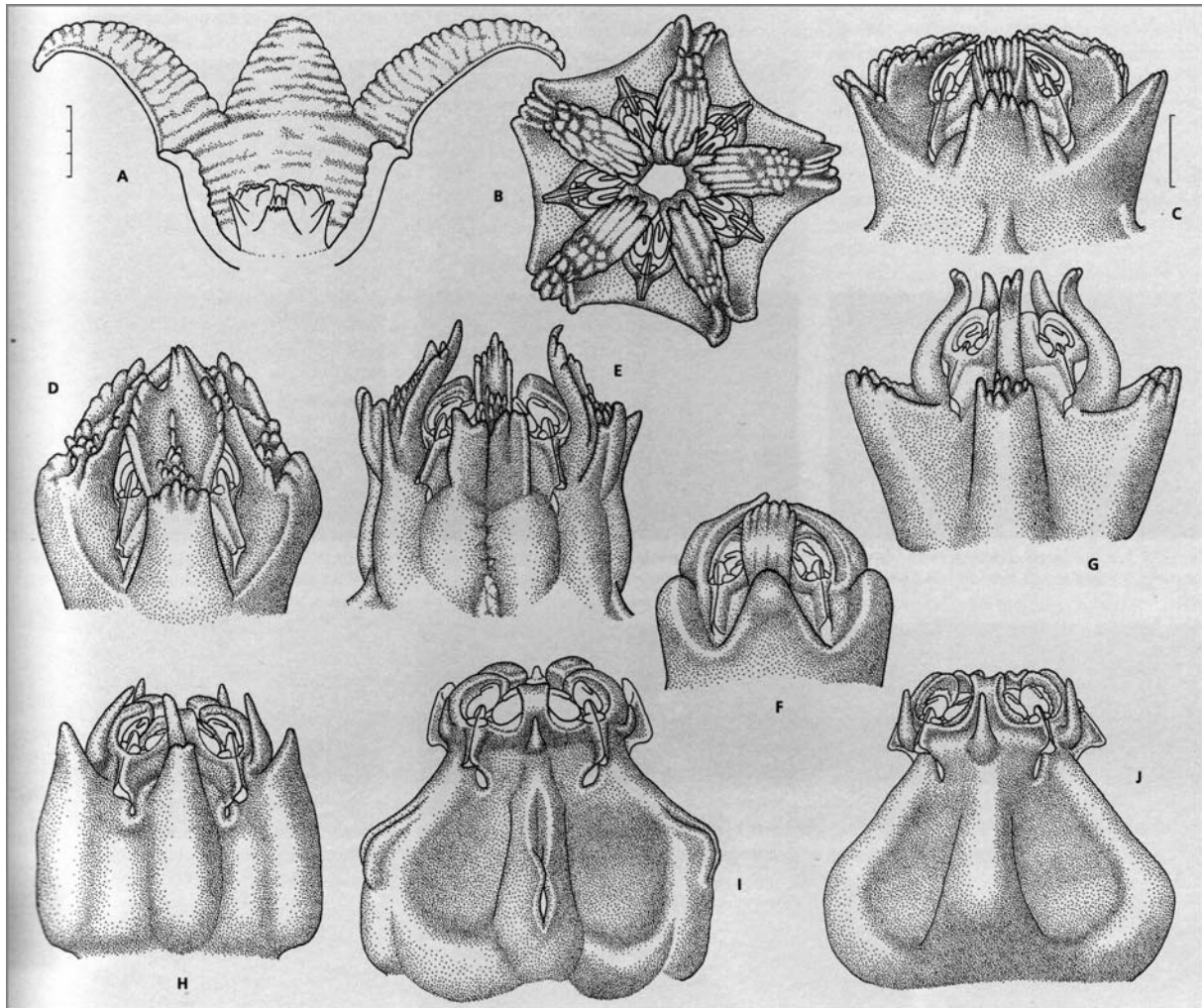


Fig. 12.15. *Piaranthus punctatus* (A-F, var. *punctatus*; G-I intermediates with var. *framesii*; J, var. *framesii*). A, side view of dissected flower. B, face view of gynostegium. C-J, side view of gynostegium. Scale bars: A, 3 mm; B-J, 1 mm (at C). Drawn from: A-C, PVB 197, Liebendal, west of Vredendal; D, Bayer & Bruyns sub KG 56/77, Gannaga Pass; E, PVB, Sout River Bridge, north of Vanrhynsdorp; F, PVB 4020, west of Middelpoort; G, J, PVB 6070, Blompoot, south-west of Loeriesfontein; H, I, PVB 6821, foot of Ezelskop, north of Nieuwoudtville.

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Fig. 12.16. *P. punctatus* var. *punctatus*, PVB 6028, Knersvlakte, north of Vanrhynsdorp.



Fig. 12.17. *P. punctatus* var. *punctatus*, PVB 4589, Soutfontein, west of Garies.

Diagnostic features and relationships

In var. *punctatus* the flowers are white to cream, usually transversely and often very boldly barred with maroon. Very occasionally they may have only short, broken transverse maroon lines changing to spots in the tube and towards the tips of the lobes. Plain, pale yellow flowers were once recorded in the Bloukrans Pass south of Calvinia. The corolla tube is cupular, 4-6 mm deep and somewhat deeper than the height of the corona but it is not at all pentagonal around its mouth. The inside of the corolla, on the lobes and around the mouth of the tube, is covered

with small and very variably shaped papillae. These are usually conical and acute but Bayer & Plowes (1975a: 75) reported spherical ones in specimens of var. *punctatus* from the Ceres Karoo and I have also found spherical ones in material from near Middelpoort, from south-west of Loeriesfontein and from around Tulpfontein in the south-western Ceres Karoo (fig. 27 B).

The bright yellow corona is tall and sometimes almost cylindrical. It is at the same time one of the most complex coronas found in the stapeliads and also one of the most variable. Some of the variation that has been seen is shown in fig. 12.15 C-F. The outer corona produces conspicuous, ascending crests behind

the inner lobes which are usually much divided and tuberculate but very occasionally can be smooth and rounded (fig. 12.15 F). The broad and flattened, often much fluted and ridged inner lobes are adpressed to the backs of the anthers but may rise quite steeply towards the centre. If the gynostegium is dissected, it will be found that the guide-rails (as is typical in *Piaranthus*) project over the mouth of a broad cavity which leads down nearly to the base of the gynostegium and is formed by the outer corona (fig. 30 E). From the outside the mouth of this cavity is sometimes visible as a small hole just below the guide-rails.

The corolla tube and tall, complicated corona make var. *punctatus* mostly unmistakable within *Piaranthus*, except *vis-a-vis* '*P. framesii*', which is discussed below. However, there are cases where the tube becomes shallow and these have been seen particularly in a swathe of territory running from Kliprand to north-west of Loeriesfontein (see fig. 12.53). Over most of this area it seems to merge into *P. cornutus*. These cases would benefit from further investigation. The fact that these species are never sympatric suggests that even *P. punctatus* might just be a more tubular-flowered form of one of the 'flat-flowered' taxa.



Fig. 12.18. *P. punctatus* var. *punctatus*, PVB 4276, Ceres Karoo near foot of Gannaga Pass, with unusually slender lobes.



Fig. 12.19. *P. punctatus* var. *punctatus*, PVB 4276, Ceres Karoo near foot of Gannaga Pass, with very finely spotted flowers.



Fig. 12.21. *P. punctatus* var. *punctatus* - *P. cornutus* intermediate, PVB 7944, north of Loeriesfontein. Here the shallow tube, the colouring and the longer inner corona show quite clearly the influence of *P. cornutus*.



Fig. 12.20. *P. punctatus* var. *punctatus*, PVB 4589, Soutfontein, west of Garies.

History

It is not known precisely when or where Masson originally found his *Stapelia punctata* but it flowered in his garden in Cape Town in 1790. His figure of this species is not very precise, but shows a finely spotted corolla with a distinctly cupular tube. This presents somewhat of a problem since Masson collected his plant in Namaqualand, where finely spotted forms are rare. As a consequence this figure cannot be said beyond all doubt to represent what is today known as *P. punctatus*, although this is now widely accepted as the correct name for them.

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Fig. 12.22. *P. punctatus* var. *punctatus*, PVB 5284, west of Kliprand. Here the tube is shallower than usual, suggesting the influence of *P. cornutus*.



Fig. 12.23. *P. punctatus* var. *punctatus*, PVB 7875, north-west of Loeriesfontein, with unusually darkly coloured flowers shallow tube suggesting the influence of *P. cornutus*.



Fig. 12.24. *P. punctatus* var. *punctatus* - *P. cornutus* intermediate, PVB 7944, north of Loeriesfontein. In these flowers the colouring is a little more like that of *P. punctatus*.

3b. *Piaranthus punctatus* var. *framesii*

Piaranthus punctatus var. *framesii* (Pillans)

Bruyns, comb. et stat. nov.

Piaranthus framesii Pillans, *S. African Gard. & Country Life* 18: 62 (1928, special reprint).

Lectotype (selected here): South Africa, Cape, Vanrhynsdorp distr., Ross Frames sub NBG 1283/26 (BOL, holo.; NBG, iso.).

Corolla 17-23 mm diam; inside covered with fine $\pm$ spherical to ovoid-acute papillae; **tube** often slightly constricted towards and always distinctly pentagonal at mouth; **lobes** eciliate. **Corona** 4.0-5.5 mm tall, 4.5-5.5 mm broad, strongly pentagonal when viewed from above from broad obtuse swellings on staminal tube towards base; **outer lobes** absent and not forming crest behind inner lobes; **inner lobes** 0.5-1.5 mm long, $\pm$ 0.5 mm broad (sometimes absent), adpressed to backs of anthers to $\pm$ erect, slender, terete and horn-like, tapering to finely acute tip.

Distribution and habitat

Apart from a collection by Harry Bolus from north of Vanrhynsdorp (Bolus 276 (BOL)), var. *framesii* has always been found a little further east and north-east, in the triangle between Loeriesfontein, Calvinia and Nieuwoudtville, i.e. on the north-eastern extremity of the Knersvlakte and on the hills and the plateau adjoining this area.

As in var. *punctatus*, plants are frequently associated with colonies of *Ruschia spinosa* but also grow under bushlets of *Pteronia glomerata* or other small shrubs. They are generally found in flatish, sometimes stony areas and they often grow with a wealth of other stapeliads.

Diagnostic features and relationships

In var. *framesii* the corolla is distinctly transversely barred with maroon or purple-brown on a whitish background on the lobes, with these bars often changing to small round spots in the base of the tube and then merging into a narrow band around the corona. In unusual cases the whole corolla is finely spotted. The barring generally becomes more intense towards the tips of the lobes and sometimes coalesces there into an almost uniform maroon patch that is usually relatively pale in colour. The inside of the corolla, mainly on the lobes and up to the mouth of the tube, is covered with small spherical to ovoid-acute papillae exactly as are sometimes found in var. *punctatus*.

The corolla tube is always obviously pentagonal, with the broadest parts opposite the guide-rails and the middle of the corolla lobes and the narrower areas between them coming close to or even touching the edges of the gynostegium. The corners of this pentagon run into the lobes, which are concave inside in their

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Fig. 12.25. *Punctatus-framesii* intermediate, PVB 6821, foot of Ezelskop, north of Nieuwoudtville, slightly pentagonal tube.



Fig. 12.26. *Punctatus-framesii* intermediate, PVB 6821, north of Nieuwoudtville, the corona is not as in var. *framesii*.



Fig. 12.27. *Punctatus-framesii* intermediate, PVB 6070, corona not as in var. *framesii*.



Fig. 12.28. *Punctatus-framesii* intermediate, PVB 4310, north-west of Calvinia, corona not as in var. *framesii* and tube only slightly pentagonal.



Fig. 12.29. *Punctatus-framesii* intermediate, PVB 6821, foot of Ezelskop, north of Nieuwoudtville. Here the colouring of the flower and shape of the tube is more suggestive of var. *framesii*, but the corona is more similar to var. *punctatus*.

lower halves.

The specimen collected by Ross Frames and designated as the type was clearly illustrated in Pillans (1928). In this the gynostegium is strongly pentagonal when viewed from above, with five rounded and somewhat laterally flattened, wing-like extensions spreading outwards near the base beneath the anthers. Between these, the gynostegium is much narrower. When viewed from the side, the gynostegium could be seen to have no inner corona lobes at all and, from a relatively narrow breadth at and immediately below the anthers, it widens considerably towards the base. As well as the lack of inner lobes, there is also no 'dorsal crest', which is normally found just behind the inner lobes. The anthers sit, therefore, exposed at the narrow top of the bright yellow gynostegium. In many plants of var. *framesii* there are actually small, slender inner corona lobes. These are usually terete and horn-like but are slender and much narrower than the anthers. Whether or not these slender inner lobes are present, this structure is markedly different in outward appearance from that in any of the other species traditionally placed in *Piaranthus*, where the gynostegium varies a little in height and breadth but hardly at all in structure.

In what ways does this structure differ internally from that found in other species of *Piaranthus*? If one sections the gynostegium of var. *framesii*, one finds that, where normally in *Piaranthus* the guide-rail is situated directly above the outer wall of the nectarial cavity, here the nectarial cavity is long and very narrow, more or less flattened against the staminal tube (fig. 30 F). Consequently the guide-rails project considerably further outwards than is usual, well beyond this outer wall (fig. 34 E). The almost hollow area between the vascular trace of the anther and the inside of the staminal tube is much broader than normal, especially towards the base. The gynostegium is also slightly taller than in *P. punctatus* and the style-head has a long, slender neck tapering gradually towards the tips of the ovaries.

This remarkable structure, despite differing from that in all other *Piaranthus* by so many



Fig. 12.30. *Punctatus-framesii* intermediate, PVB 6070, Blompoort, south-west of Loeriesfontein, corona not as in var. *framesii*.



Fig. 12.31. *P. punctatus* var. *framesii*, PVB 4328, Loeriesfontein, but with an unusually bold colour.



Fig. 12.32. *P. punctatus* var. *framesii*, PVB 6821, foot of Ezelskop, north of Nieuwoudtville.

features, does not remain constant. In several distinct localities, especially north-east of Nieuwoudtville, intermediates between var. *framesii* and var. *punctatus* have been located. These were first collected by M. Bruce Bayer in 1972 near Grasberg and have since been recorded in the grid-squares 3019 CC (PVB 6070 (BOL)), 3119 AA (PVB 6821 (NBG)), 3119 AD (PVB 7977 (MO)) and 3119 BC (PVB 7846 (K)). In some of the plants the flowers have a 'punctatus-like' corona in which the corolla tube is conspicuously pentagonal. In others, the inner corona lobes, which are broad in var. *punctatus*, are slender and practically terete, without any dorsal ridges or bumps, though they still exceed the anthers. In yet other specimens the outer coronal crest below them becomes smaller and lower on the gynostegium, moving down to near the bases of the guide-rails, then right away from them (as shown in Meve 1994, fig. 21 E, G).

Meve mentioned that the two species '*P. framesii*' and *P. punctatus* 'display a considerable degree of vicariance but are also most likely genetically incompatible' (p. 96). According to his distribution map (fig. 22), the distribution of '*P. framesii*' is nested within that of *P. punctatus*. In his account '*P. framesii*' was recorded in eight quarter-degree squares and in four of these *P. punctatus* was recorded as well (Meve 1994). In a further three of these (3019 CD, 3119 BC, 3119 DB), *P. punctatus* has actually been recorded as well. Therefore spatially they are not vicariant taxa. Ecologically the higher-lying parts towards the east of the area where var. *framesii* occurs are relatively uniform and both taxa occur together here under very similar ecological circumstances. Consequently in this area at least they are not ecologically vicariant either. Further to the west the country is very dissected and var. *framesii* often grows here at higher altitudes than var. *punctatus* so that here it could be claimed that they are ecologically vicariant. As far as their incompatibility is concerned, Meve found them to be partly inter-sterile (Meve 1994: Table 3). However, my own pollination experiments have found them to be easily crossed in both directions and this is borne

out by the experience of Bayer (1999), who also found them to be inter-fertile. In addition, Meve (1994) believed that the spherical papillae on the inside of the corolla in '*P. framesii*' were 'unique within the whole genus' (p. 93). In this regard it should first be observed that, in his fig. 21 D and I, about half of the papillae shown for '*P. framesii*' are not spherical and cannot be separated from those in fig. 23 G of *P. punctatus*. Secondly, as Bayer & Plowes (1975a: 75) pointed out, spherical papillae are found in *P. punctatus* in areas where '*P. framesii*' does not occur at all. Consequently, they are not a unique feature of '*P. framesii*'.

Bayer & Plowes (1975a) concluded that *P. punctatus* and '*P. framesii*' were two distinct species but that further observations would be needed to determine their actual relationship. Meve's (1994) account of the two does not address this problem. My own exploration has revealed that '*P. framesii*' mostly occurs in association with *P. punctatus* and does not appear to exist independently of it, that there is no significant barrier of sterility between them and that they are connected morphologically in

several localities by a range of intermediates. Thus, if careful collecting is done, many plants will be found that cannot be placed unequivocally under '*framesii*' or '*punctatus*'. In the light of this information, there seems to be no option but to consider them as varieties of a single species and that is the approach taken here.

History

Percival 'Percy' Ross Frames, a solicitor and one-time director of De Beers, discovered var. *framesii* in the Vanrhynsdorp district in 1926. The identity of var. *framesii* was confused in White & Sloane (1937) and Lückhoff (1952) and the cause of this seems to have been the plate by H. Lang which was published in *Flowering Plants of South Africa* (Phillips 1935b). Bayer & Plowes (1975a) were the first to sort out this confusion and they demonstrated that this plate was of var. *punctatus* and not of var. *framesii*.

Pillans (1928) actually cited two specimens collected by Ross Frames (NBG 1283/26 and 1284/26) and so it is necessary to select a lectotype, which is done here.



Fig. 12.33. *P. punctatus* var. *framesii*, PVB 6070, Blompoort, south-west of Loeriesfontein.

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4. *Piaranthus geminatus*

Piaranthus geminatus (Masson) N.E.Br., *J. Linn. Soc. Bot.* 17:163 (1878).

Stapelia geminata Masson, *Stap. Nov.*: 18, t. 25 (1797).
Obesia geminata (Masson) Haw., *Syn. Pl. Succ.*: 42 (1812).

Podanthes geminata (Masson) G.Nichols., *Ill. Dict. Gard.* 3:172 (1886).

Caralluma geminata (Masson) Schltr., *J. Bot.* 36: 478 (1898).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 25.

Stems 10-60 (-150) mm long, 8-20 (-25) mm thick, globose to subglobose, pale to dark grey-green, smooth to papillate; **tubercles** with apical deltoid leaf-rudiment 0.3-1.2 mm long, usually with 2 minute stipular denticles at base. **Pedicel** 2-20 mm long, 1-2 mm thick; **sepals** 2-4 mm long, 0.5-1.2 mm broad at base. **Corolla** (15-) 20-42 mm diam., rotate; inside white, yellow, yellow-green or brown, transversely marked with red to brown, rarely uniformly yellow or red-brown, covered with fine slender conical-acute papillae < 1 mm long; **tube** ± absent; lobes 8-18 mm long, 3-5 (-6.5) mm broad at base, spreading, ovate to deltate, acute, with margins recurved, rarely with few clavate cilia up to 2 mm long near base. **Corona** 2.3-3.5 mm tall, 3.2-6.5 mm broad, yellow sometimes spotted with red; **outer lobes** forming narrow platform to ± absent below guide-rails, forming rounded to deeply rugulose-tuberculate crest to 1.0-2.2 mm broad behind inner lobes; **inner lobes** 1-2 mm long, 0.5-1.2 mm broad, adpressed to backs of anthers and usually exceeding them but not ascending beyond them, ovate-deltoid to linear, acute to denticulate.

4a. *Piaranthus geminatus* subsp. *geminatus*

Piaranthus disparilis N.E.Br., *Fl. Cap.* 4 (1): 1021 (1909).

Type: Cape, between Ladismith and Laingsburg, *N.S. Pillans* 57 (K, holo.; BOL, iso.).

Piaranthus foetidus N.E.Br., *Fl. Cap.* 4 (1): 1021 (1909).
Piaranthus geminatus var. *foetidus* (N.E.Br.) Meve, *Bradleya* 12: 84 (1994).

Type: Cape, 9 miles east-south-east of Bedford, *N.S. Pillans* 165 (K, holo.; BOL, GRA, iso.).

Piaranthus foetidus var. *diversus* N.E.Br., *Fl. Cap.* 4 (1): 1022 (1909).

Type: Cape, across Sundays R. near Graaff-Reinet, *N.S. Pillans* 142 (K, holo.; BOL, GRA, iso.).

Piaranthus foetidus var. *multipunctatus* N.E.Br., *Fl. Cap.* 4(1): 1022 (1909).

Type: Cape, near Graaff-Reinet, Wheatlands, E. *Pillans sub N.S. Pillans* 695 (K, holo.; BOL, iso.).

Piaranthus foetidus var. *pallidus* N.E.Br., *Fl. Cap.* 4 (1): 1022 (1909).

Type: Cape, east of Graaff-Reinet, *N.S. Pillans* 111 (K, holo.; BOL, iso.).

Piaranthus foetidus var. *purpureus* N.E.Br., *Fl. Cap.* 4 (1): 1022 (1909).

Type: Cape, near Graaff-Reinet, Wheatlands, E. *Pillans sub N.S. Pillans* 698 (K, holo.; BOL, iso.).

Piaranthus pillansii N.E.Br., *Fl. Cap.* 4 (1): 1019 (1909).

Type: Cape, hills near Oudtshoorn, *N.S. Pillans* 691 (K, holo.; BOL, iso.).

Piaranthus pillansii var. *fuscatus* N.E.Br., *Fl. Cap.* 4 (1): 1020 (1909).

Type: Cape, 9 miles from Oudtshoorn to George, E. *Pillans sub N.S. Pillans* 686 (K, holo.; BOL, iso.).

Piaranthus pillansii var. *inconstans* N.E.Br., *Fl. Cap.* 4 (1): 1019 (1909).

Type: Cape, hills near Oudtshoorn, *N.S. Pillans* (K, holo.).

Piaranthus disparilis var. *immaculatus* C.A.Luckh. in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1145 (1937).

Lectotype: White & Sloane, *Stap.*, ed. 2, 2: fig. 811.

Piaranthus globosus A.C.White & B.Sloane, *Stap.*, ed. 2, 2: 814 (1937).

Type: cultivated material of unknown origin, *White & Sloane* 53-1 (missing). Lectotype: White & Sloane, *Stap.*, ed. 2, 2: fig. 823.

Piaranthus barrydalensis Meve, *Bradleya* 12: 68 (1994).

Type: South Africa, Cape, east of Barrydale, Klein-doonrivier, Meve et al. 128 (K, holo.; MSUN, iso.).

Stems ± smooth.

The westernmost of the elements of *P. geminatus* in the Little Karoo is what was named *P. barrydalensis*. This occurs on the western margin of the Little Karoo from about 20 km north of Montagu to east of Barrydale. In the last decade more collections have been made in this area and further north-eastwards, nearer to Touws River.

Plants grow in locally arid spots in valleys and the lower slopes of hills among low, karroid vegetation, often with *Pteronia paniculata* and various succulent shrublets.

Meve mentioned that 'in the east *P. barrydalensis* is sympatrically distributed with the small-flowered form of *P. geminatus* var. *geminatus*'. According to his distribution map (fig. 14) and the material that he cited, there are two collections of var. *geminatus* which were made in the quarter-degree squares 3320 DC and DD where *P. barrydalensis* occurs. However, one of these (Lavranos & Pehlemann 15749) was actually made in 3320 BD, which is not anywhere near where *P. barrydalensis* occurs. The other (Hall sub NBG 835/53) was made near Barrydale and is indicated on the map as belonging to 'forma *fuscatus*'. This is a name which Meve (p. 87) used to cover the 'rather large and red-flowered individuals, scentless but often with speckled corona.. .[which] characterise the transition zone [of var. *geminatus*] with var. *foetidus*' east of Oudtshoorn. However, in this specimen the flower is not especially large and there is no reason why it should not have been included under *P. barrydalensis*. There is therefore no evidence of sympathy between *P. barrydalensis* and forms of *P. geminatus*. The records show that *P. barrydalensis* is mainly somewhat isolated to the west of the driest, low-lying areas of the western Little Karoo along the valley of the Touws River.

In *P. barrydalensis* the stems are rounded and practically without any angles, often more

Key to the subspecies of *P. geminatus*

- Stems more or less smooth 4a. subsp. *geminatus*
Stems finely but noticeably papillate 4b. subsp. *decorus*

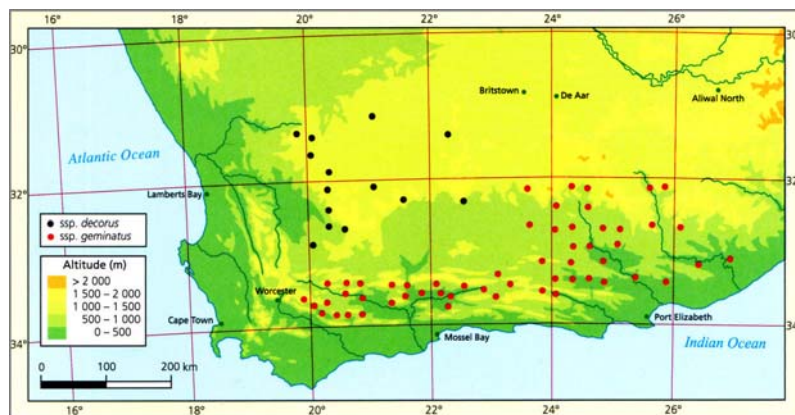


Fig. 12.34. Distribution of *Piaranthus geminatus*.



Fig. 12.35. *P. geminatus* subsp. *geminatus*, PVB 5150, Montagu (f. *disparilis*).



Fig. 12.36. *P. geminatus* subsp. *geminatus*, PVB 5150, Montagu (f. *disparilis*).



Fig. 12.37. *P. geminatus* subsp. *geminatus*, PVB 5150.

or less 'globose'. This taxon is mainly recognised by the relatively small flowers (20-26 mm in diameter) with broad lobes (5-6 mm) and the 'coarse dark red-brown bands on a rather whitish corolla' (Meve 1994: 71). In my own collections several plants have been sampled at each locality and the colour of the inside of the flowers has proved to be exceptionally variable. Some have coarse, dark, purplish red bands on whitish as in the type but many have deep red bands on cream with a patch of red at the apex of each lobe. Yet others have very fine, dark bands so that the flower is almost cream in overall colour. Among some of these collections are also plants with fine transverse stripes or even spots lower on the lobes changing to a dark purple-red or nearly black patch around the apices. These bear strong resemblance to specimens found at the eastern end of this complex which are usually attributed to '*foetidus*'.

The first record of plants from around Barrydale seems to have been made by Percy Ross Frames in 1928 (White & Sloane 1937:811), though no photograph or specimen exists from this collection. The next recorded collection is that of H. Hall which was made in 1953.

As one moves further east in the Little Karoo, the next element in this complex is soon encountered and it is particularly common under small bushes on shales and tillites in dry places around the foot of the Anysberg, Warmwaterberg, Touwsberg and around the western corner of the Klein Swartberg. As with *P. barrydalensis*, these plants have characteristically rounded, 'globose' stems. Here the flowers are smaller than in var. *geminatus* and of the same size

as in *P. barrydalensis* (both in diameter of the flower - though some with flowers as small as 12 mm diameter have been found - and in the width of the lobes, consequently possessing the same relatively broad buds). They are mostly a uniform, dullish, pale yellow or cream inside but are often faintly flushed with pink. Generally the inside of the flower is without any transverse red markings but in some populations (e.g. PVB 7348 from Hondewater along the Toub River) there is a wide range from flowers without any transverse markings to others where they are present. Such plants are almost identical, both vegetatively and florally, to White & Sloane's *Piarranthus globosus*, which they described but did not know the origin of. In most localities where this form has been collected, a few plants also occur with faintly to boldly striped flowers just as in *P. barrydalensis*. The papillae on the corolla are often quite conspicuous, especially in a patch towards the tips of the lobes. A few specimens have been seen with marginal cilia along the lobes. As far as can be seen, these specimens differ from *P. barrydalensis* only in the lack of the dark red lines on the corolla. Meve designated these as *P. geminatus* var. *geminatus* forma *disparilis*.

Plants of this form were first observed by N.S. Pillans between Ladismith and Laingsburg in November 1904 and these were described by N.E. Brown as *Piarranthus disparilis*.

Further to the east, from Ladismith to near Willowmore, one finds the taxon which is best known by the name *P. pillansii*. This was placed under *P. geminatus* var. *geminatus* by Meve (1994), as he considered them to be the best match for Masson's figure of the much earlier

name *Stapelia geminata*. Meve also cited a few localities for it in the Great Karoo as far afield as Loxton and the Karoo National Park at Beaufort West. However, it seems far more probable that these collections refer to plants of subsp. *decorus* with unusually coloured flowers and that subsp. *geminatus* occurs much further south and east on the Little and Great Karoo.

These plants grow mainly in flat, gravelly patches under small bushes, usually with a wide variety of other small succulents.

The stems are still usually rounded, with very obscure tubercles and without obvious angles but they are no longer globose and tend to be much longer than broad.

In these the flowers are relatively large at 25-35 mm in diameter (but up to 42 mm on occasion) often, though not always, with slender lobes that attenuate gradually towards their tips. The colour of the flowers varies from pale yellow faintly dusted with fine red spots to darker red towards the tips with a yellowish centre. Plants from the eastern edge of this area (De Rust to Uniondale and Willowmore) tend to exhibit less rounded stems with much more prominent tubercles and they have also darker and more intensely coloured flowers. These were designated as *P. geminatus* var. *geminatus* forma *fuscatus* by Meve (p. 87) and he regarded them as transitional between his var. *geminatus* and var. *foetidus*.

East of var. *geminatus* (and to a large degree outside the Little Karoo entirely), from Murraysburg and Aberdeen to north-east of Grahamstown and further south from Willowmore to Addo near Port Elizabeth, one finds *P. geminatus* var. *foetidus*. This was first gathered



Fig. 12.38. *P. geminatus* subsp. *geminatus*, PVB 7829, south-east of Montagu (f. *disparilis*).



Fig. 12.39. *P. geminatus* subsp. *geminatus*, PVB 3737, north-west of Barrydale (f. *disparilis*).



Fig. 12.40. *P. geminatus* subsp. *geminatus*, PVB 7348, Hondewater. Plants with flowers as in PVB 3737 were also found here (f. *disparilis*).

PIARANTHUS GEMINATUS



Fig. 12.41. *P. geminatus* subsp. *geminatus*, PVB 6384, near Avondrust (f. *disparilis*).



Fig. 12.42. *P. geminatus* subsp. *geminatus*, PVB 7530a, northern foot of Warmwaterberg (f. *disparilis*).



Fig. 12.43. *P. geminatus* subsp. *geminatus*, PVB 2195, near Studtis (f. *foetidus*).



Fig. 12.44. *P. geminatus* subsp. *geminatus*, PVB 7074, between Uniondale and Willowmore, (f. *fuscatus*).



Fig. 12.45. *P. geminatus* subsp. *geminatus*, PVB 2195, near Studtis, Baviaanskloof (f. *foetidus*).



Fig. 12.46. *P. geminatus* subsp. *geminatus*, PVB 2195, near Studtis (f. *foetidus*).

by N.S. Pillans near Bedford in July 1903.

In var. *foetidus* the stems are usually short and stout and are clearly 4-angled, bearing obvious tubercles so that they are consequently not at all rounded.

The flowers are 18-30 mm in diameter, with relatively broad lobes 5-7 mm across which are broader relative to their diameter than is the case for var. *geminatus*. The corolla is sometimes boldly transversely striped with brown (more rarely with red) on white to dark yellow and the dark colour often coalesces into an apical brown (or red) patch on each lobe. In many cases they are very finely dusted with brown, without any transverse bands being visible, with a darker patch in the apical half that fades gradually towards the centre.

Var. *foetidus* and var. *geminatus* (the forma *fuscatus*) occur together between Willowmore and Uniondale (in the quarter-degree square 3323 AD) but are not otherwise sympatric. Where they occur together it may be difficult to tell them apart.

It is not at all clear why *P. barrydalensis* was separated from the rest as a distinct species. According to Meve, 'concentrating one's attention on the colour and pattern of the corolla and the corona, on the indumentum and the totally different odours, there seems to be no direct relationship between' *P. barrydalensis* and var. *geminatus*. As far as its relationship to var. *foetidus* is concerned, he mentioned that the smell is 'foetid but more fruity' and var. *foetidus* differs otherwise 'in the colouring and indumentum of the corolla, the late flowering time, the stems and at least the en bloc habitat in the eastern Cape'.

As far as the indumentum is concerned,

Meve showed it to be particularly variable in both varieties of *P. geminatus*. However, even with the best will in the world, it is impossible to see the difference between the papillae in fig. 6 E, H (*P. barrydalensis*), fig. 15 D, H (var. *geminatus*) and figs. 16 D, 17 M (var. *foetidus*) in Meve (1994), so this character does not separate them. As far as the stems are concerned, there is a cline from rounded and globose in the west to rounded and more elongated further east and to clearly tuberculate and elongated still further east. In this respect, *P. barrydalensis* fits into the western part of this cline and is no different from the stems found in his *P. geminatus* var. *geminatus* f. *disparilis*. The colour of the flower has also been found to be variable and plants of his *P. geminatus* var. *geminatus* f. *disparilis* can be found whose flowers match

the colour in *P. barrydalensis*. So the only difference lies in the supposedly 'totally different odours' and it is felt that this is not enough to base a species on.

It seems most logical to treat this complex as a single taxon. From Montagu eastwards there is more or less continuous variation in all the various characters of the stems and flowers and there are no clear discontinuities. The only remaining problem is, at what rank should the different elements be recognised, if indeed they can be recognised at all. The informal rank of 'forma' as assigned by Meve (1994) seems most appropriate: f. *disparilis* in the west (including *P. barrydalensis*), f. *geminatus* between Ladismith and Oudtshoorn, f. *fuscatus* east of Oudtshoorn and linking up with f. *foetidus* in the east and north-east.



Fig. 12.47. *P. geminatus* subsp. *geminatus*, PVB 3062, near Aberdeen (f. *foetidus*).

4b. *Piaranthus geminatus* subsp. *decorus*

Piaranthus geminatus subsp. *decorus* (Masson)

Bruyns, comb. et stat. nov.

Stapelia decora Masson, Stap. Nov.: 19, t. 26 (1797).

Obesia decora (Masson) Haw., Syn. Pl. Succ.: 43 (1812).

Orbea decora (Masson) Steud., Nomencl. Bot., ed. 2, 2: 222 (1841).

Piaranthus decorus (Masson) N.E.Br., J. Linn. Soc. Bot. 17:163 (1878).

Caralluma decora (Masson) Schltr., J. Bot. 36: 478 (1898).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, Stap. Nov.: t. 26.

Stapelia serrulata Jacq., Stap.: t.17 (1806-19).

Obesa serrulata (Jacq.) Sweet, Hort. Brit., ed. 1: 278 (1826).

Caruncularia serrulata (Jacq.) G.Don, Gen. Hist. 4:122(1837-8).

Piaranthus serrulatus (Jacq.) N.E.Br., J. Linn. Soc. Bot. 17:163 (1878).

Caralluma serrulata (Jacq.) Schltr., J. Bot. 36: 478

Lectotype: Jacq., Stap.: t.17.

Caruncularia serrata Haw. ex Decne. in DC, Prodr. 8:658 (1844), pro syn.

Stems finely but noticeably papillate.

In the north subsp. *decorus* is found along the eastern foot of the Hantamberge, north-east of Calvinia, eastwards to near Williston. It has been found sporadically along the Roggeveld plateau southwards to near Fraserburg and is also recorded in the eastern Ceres Karoo along the foot of the escarpment. There are also a few records from around Beaufort West.

Subsp. *decorus* is found in stony, flattish pots on shales or patches of metamorphosed shale near dolerite outcrops and occasionally among dolerite stones. Plants are frequently associated with colonies of spiny *Ruschia*, where they grow under these shrublets with other stapeliads such as *Duvalia caespitosa*, *D. maculata*, *Quaqua acutiloba* and *Q. marlothii* as well as *Senecio radicans*.

The stems of subsp. *decorus* are more papillate than is usually the case in *Piaranthus* but they are otherwise typical.

Here the corolla is more or less flat with the lobes slightly reflexed towards their tips and it is generally between 15 and 30 mm in diameter. The lobes are relatively broad (at 4-5 mm), tapering fairly quickly to their tips which are not attenuated. The background colour of the corolla is cream to yellow and on this background there are many fine red-brown bars which are longest around the middle of the lobe, becoming smaller and finer towards the centre. Towards the tip of the lobe they tend to become coarser and very occasionally they coalesce there into a red-brown patch.

The bright yellow corona has a particularly broad crest, which is between 1.4 and 2.0 mm wide, behind each inner lobe and the inner corona lobes are always adpressed to the backs of the anthers for the whole of their length.

Meve (1994) considered this taxon and *P. cornutus* to belong to a single species within which he recognised them as two subspecies. He mainly discussed the relationship between these two subspecies. However, subsp. *decorus* is very similar in many respects to *P. geminatus* and it seems probable that some of the records *P. geminatus* from outside the Little Karoo may actually refer to subsp. *decorus* (which is where they are placed here). It seems that he considered the papillate stems in subsp. *decorus* to separate it adequately from *P. geminatus*. However, florally there is little on which they might be separated. The flowers have the same shape. In *P. geminatus* the coronal crest behind the inner lobes varies from 1.2 to 2.2 mm broad



Fig. 12.48. *P. geminatus* subsp. *decorus*, PVB 4886a, north of Williston (growing together with *P. cornutus* var. *cornutus*).

so its breadth in subsp. *decorus* easily fits within these limits and is not sufficient so separate them. I can find no reason not to include subsp. *decorus* under *P. geminatus* at subspecific level, with the more papillate stems being the main criterion separating the two subspecies.



Fig. 12.49. *P. geminatus* subsp. *decorus*, Theron, Tafelberg, south-west of Fraserburg, looking very like some flowers of subsp. *geminatus* from the Little Karoo (growing together with *P. cornutus* var. *cornutus*).



Fig. 12.50. *P. geminatus* subsp. *decorus*, PVB 3041, north-west of Sutherland.

PIARANTHUS CORNUTUS

5. *Piранanthus cornutus*

Piранanthus cornutus N.E.Br., Fl. Cap. 4 (1): 1018 (1909).

Piранanthus decorus subsp. *cornutus* (N.E.Br.) Meve, *Bradleya* 12: 76 (1994).

Type: South Africa, Cape, Little Namaqualand, June 1874, *Barkly* 25 (K).

Stems 10-60 (-150) mm long, 8-20 (-25) mm thick, globose to subglobose, pale to dark grey-green, smooth to papillate; **tubercles** with apical deltoid leaf-rudiment 0.3-1.2 mm long, usually with 2 minute stipular denticles at base. **Pedicel** 2-20 mm long, 1-2 mm thick; **sepals** 2-4 mm long, 0.5-1.2 mm broad at base. **Corolla** (15-) 20-28 mm diam., rotate, often with ascending lobes; inside white to yellow, with many fine red to red-brown dots or transverse bands, rarely uniformly white to yellow, covered with slender conical-acute papillae up to 1 mm long; **tube** $\pm$ absent; **lobes** 8-12 mm long, 3-5 mm broad at base, ascending with recurved tips to spreading, narrowly deltate, acuminate, with margins recurved, rarely with few vibratile clavate cilia up to 2 mm long near base. **Corona** 2.5-5.0 mm tall, 3.5-5.0 mm broad, yellow sometimes spotted with red-brown; **outer lobes** forming slightly to deeply rugulose-tuberculate crest to 0.8-1.5 mm broad behind inner lobes; **inner lobes** 1-2 mm long, 0.5-0.8 mm broad, adpressed to backs of anthers and exceeding them, usually steeply ascending towards centre, narrowly ovate-deltoid to linear, acute to denticulate.

Meve (1994) placed subsp. *decorus* and subsp. *cornutus* together under *P. decorus* because of their 'overall close similarities in corolla and stem morphology (rough epidermis)'. However, he also remarked that the papillate stems were of 'obviously adaptive relevance' and so the taxonomic significance of this criterion is doubtful, especially since in subsp. *cornutus* the surface is 'somewhat smoother' (p. 61). An important consideration for his treatment was also the existence of 'extremely decorus-like' individuals towards the southern end of the distribution range of subsp. *cornutus* (p. 77). He discussed this further (p. 79), mentioning that a few specimens had been recorded in this area (in the degree square 3018) in which the inner corona lobes are adpressed to the anthers and do not rise above them. As evidence for this he mentions his fig. 11 D & O, but actually these two illustrations are based on the specimen *Pehlemann* 317 which came from Rosh Pinah in Namibia (in the degree square 2716). On the distribution map (fig. 10) two of these problematic specimens are clearly marked. However, one of them (*Bruyns* 4706) is in fact a collection that is intermediate between *P. cornutus* and *P. punctatus*, so it should not be cited here. Consequently there is actually very little evidence of intermediates or intergradation between *P. cornutus* and '*decorus*'.

Meve (1994) found that subsp. *decorus* and subsp. *cornutus* were allopathic with the former 'topographically rather isolated'. As well as providing a much more representative

Key to the varieties of *P. cornutus*

Corolla spotted or barred inside with dark on cream background, inner corona lobes rising steeply in centre	5a. var. <i>cornutus</i>
Corolla without spots or bars inside, inner corona lobes not rising in centre	5b. var. <i>ruschii</i>

picture of the distribution of subsp. *cornutus*, more recent collecting has also indicated that it grows together with subsp. *decorus* in at least two areas. One of these spots is north of Williston (in the square 3121 AA, *PVB* 4886 (BOL)) and the other is between Sutherland and Fraserburg (3221 AA, *PVB* 4796 (BOL)). The two taxa appear to remain discrete in these localities.

Much of the evidence (and especially this evidence of sympatry over a fairly wide area) now lends support to the notion that in this case we are dealing with two distinct species. This is the view that I have adopted here, with subsp. *cornutus* recognised at specific level as *Piранanthus cornutus* and subsp. *decorus* placed as a subspecies under *P. geminatus*.

Piранanthus cornutus was the most widely distributed taxon in *Piранanthus* until *Huerniopsis decipiens* was moved to *Piранanthus*. It is found in southern Namibia, and from there sporadically into the western corner of the Free State. In Namibia it is found from Aus southwards (mainly in the mountains) to Rosh Pinah. East of this there are sporadic records around Klein Karas, around the foot of the Great Karas Mountains and near Warmbad. In Namaqualand it is uncommon below the escarpment, where there are only two records [*PVB* 3658 from the foot of Spektakel Pass and *PVB* 8280 from Lekkersing]. Otherwise it is far more plentiful further inland, where it is found from north of Steinkopf and in the gneiss hills around Springbok along the eastern flanks of the Kamiesberg to near Kliprand. Further eastwards it is fairly common around Pofadder but

becomes much rarer eastwards to Kakamas and Prieska. To the south of this, recent collecting has indicated that it is common between Calvinia and Williston as well as around Carnarvon. Further east it occurs rather more sporadically near Strydenburg and Britstown and even extends as far as the Free State near Lückhoff. Yet further south it has been seen very sporadically near Fraserburg but no other localities are known on the southern portion of the Roggeveld Plateau. This is a much more considerable range than was known to Meve (1994), who mentioned (p. 79) that it 'is a taxon of the winter-rainfall area (single exceptions known)'. In fact *P. cornutus* is relatively widely found in the summer-rainfall zone.

Over this large range, *P. cornutus* is found in a wide variety of habitats, from gravelly gneissic ground on flats between the domes of the Kamiesberg to patches of quartz gravel (around Warmbad, Pofadder and Klein Karas) and gravelly spots between dolerite or jasper outcrops (Williston to Strydenburg and Britstown). Whereas in these last-mentioned eastern spots plants are occasionally found associated with *Rhigozum trichotomum* [*driedoring*], over much of their range they are often associated with gregarious species of *Ruschia*. These include such spiny species as *R. spinosa* and *R. divaricata*, but also spineless ones such as *R. robusta*, which is characteristic of many of the gravelly, flat areas on the drier side of the Kamiesberg and often provides shelter for *P. cornutus*, *Quaqua acutiloba* and several other stapeliads.



Fig. 12.51. *P. cornutus* var. *cornutus*, *PVB* 4886b, north of Williston.

PIARANTHUS CORNUTUS

5a. *Piaranthus cornutus* var. *cornutus*

Piaranthus cornutus var. *grandis* N.E.Br., *Fl. Cap.* 4 (1): 1018 (1909).

Type: Cape, near Victoria West, Barkly 25 bis (K).

Piaranthus pulcher N.E.Br., *Fl. Cap.* 4 (1): 1022 (1909).

Type: without locality, received at Kew in 1876, Shaw (K).

Piaranthus nebrownii Dinter, *Neue Pflanzen Deutsch-SWAs.*: 47 (1914).

Piaranthus pulcher var. *nebrownii* (Dinter) A.C.White & B.Sloane, *Stap.*, ed. 2, 2: 797 (1937).

Type: Namibia, Klein Karas, 9 Oct. 1913, J. Dinter sub Dinter 3248 (SAM).

Piaranthus mennellii C.A.Luckh., *S. African Gard. & Country Life* 25: 96 (1935).

Type: Cape, near Pofadder, Mennell sub Lückhoff 223 (BOL).

Piaranthus pallidus C.A.Luckh., *S. African Gard. & Country Life* 25: 96 (1935).

Type: Cape, near Pofadder, Mennell sub Lückhoff 222 (BOL).

Corolla usually spotted or barred inside with red to red-brown on pale background. Inner corona lobes adpressed to backs of anthers and rising steeply towards centre.

Var. *cornutus* occurs over much of the range of the species. Here the corolla is 15-30 mm in diameter. It is rarely flat and the corolla lobes generally rise somewhat from their bases and then spread towards their tips. The lobes have an ovate base and taper from this gradually to a slender tip. Along the eastern flank of the Kamiesberg, the flowers have a creamy background and are especially boldly marked with maroon spots which become transversely elongated towards the bases of the lobes (fig. 12.56). Further east and north, the colour becomes more variable. The background is cream to white but the spots vary from bold as before to very fine and, in some cases, are even entirely absent.

The corona has a relatively small crest behind each inner lobe, which rarely exceeds 1.5 mm broad. The inner corona lobes are mostly adpressed to the anthers in their lower half, then rise above them and are sometimes apically recurved.

Var. *cornutus* was described from material sent by Henry Barkly to N.E. Brown from Little Namaqualand. N.E. Brown (1890) first included the type (and some others) under *P. decorus* but was uncertain about this and later decided that they represented a new species. Various different forms of this species have received names since then but these have all been placed in synonymy (Meve 1994).



Fig. 12.52. *P. cornutus* var. *cornutus*, PVB 4886b, north of Williston.

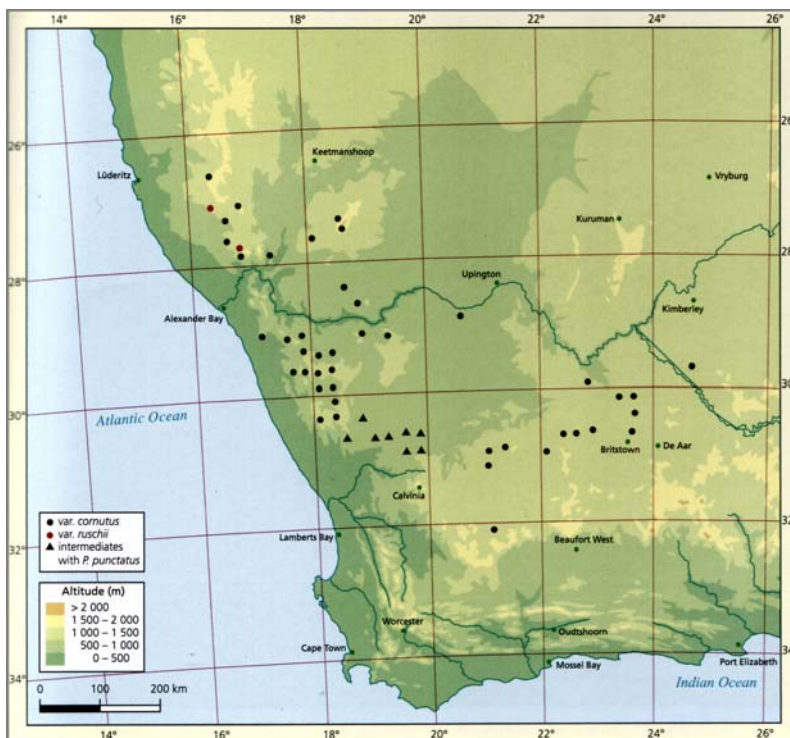


Fig. 12.53. Distribution of *Piaranthus cornutus*.



Fig. 12.54. *P. cornutus* var. *cornutus*, PVB 4886b, north of Williston.



Fig. 12.55. *P. cornutus* var. *cornutus*, PVB 7550, north of Williston.

PIARANTHUS CORNUTUS



Fig. 12.56. *P. cornutus* var. *cornutus*, PVB 6713, north-east of Kamieskroon.



Fig. 12.57. *P. cornutus* var. *cornutus*, PVB 3650, west of Grönaau, Namibia.



Fig. 12.58. *P. cornutus* var. *cornutus*, PVB 5246, north-west of Pofadder, corolla without the characteristic spots.

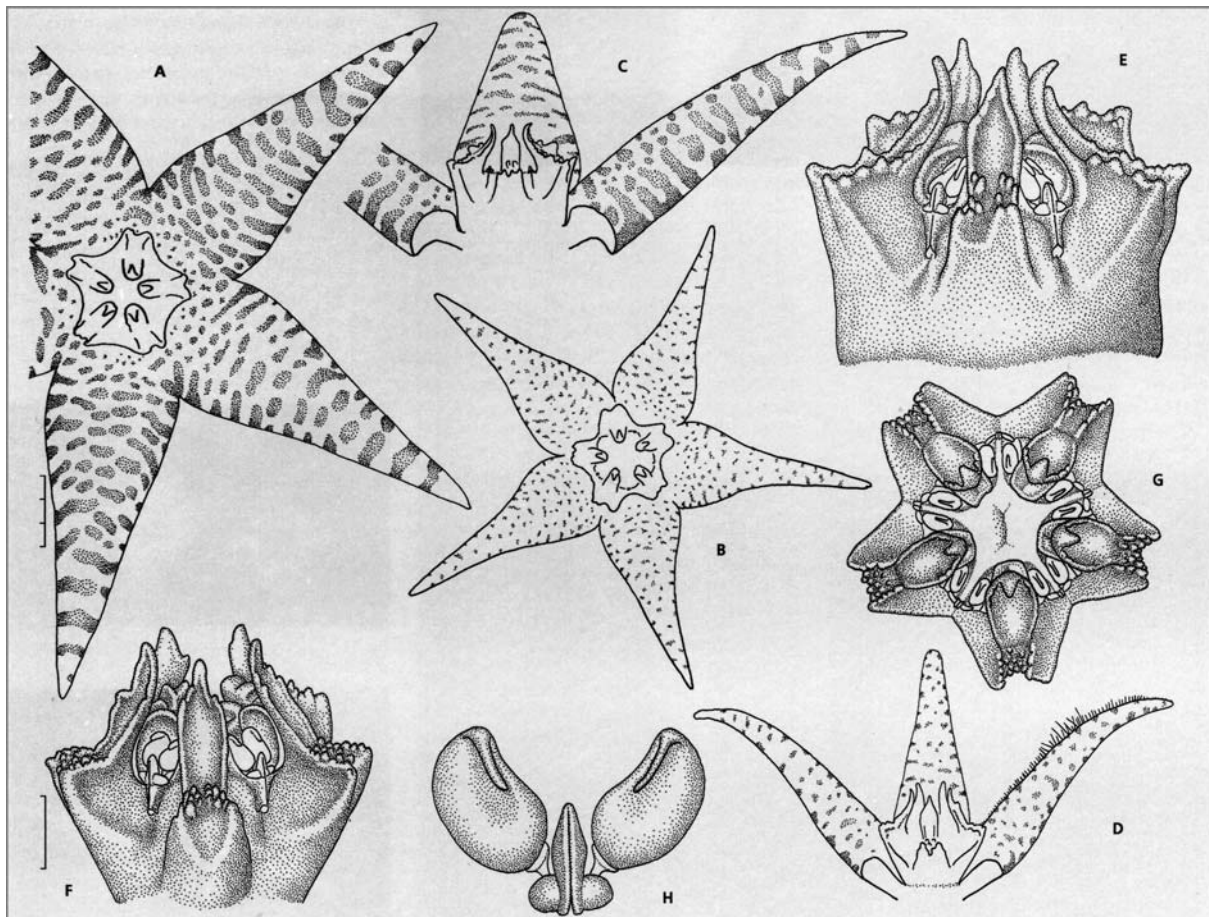


Fig. 12.59. *Piaranthus cornutus* var. *cornutus*. A, B, face view of flower. C, D, side view of dissected flower. E, F, side view of gynostegium. G, face view of gynostegium. H, pollinarium. Scale bars: A-D, 3 mm (at A); E-G, 1 mm (at F); H, 0.25 mm (at F). Drawn from: A, C, E, PVB 3658, west of Spektakel Pass; B, D, F-H, PVB 3650, west of Grönaau, Namibia.

5b. *Piaranthus cornutus* var. *ruschii*

Piaranthus cornutus var. *ruschii* (Nel) Bruyns,
comb. et stat. nov.

P. ruschii Nel in A.C. White & B. Sloane, Stap., ed.
2, 2:813(1937).

Type: Namibia, Pockenbank, *E. Rusch* (missing).

Lectotype: White & Sloane, Stap., ed. 2, 2: fig. 822.

Corolla uniformly white to pale yellow (or suffused with pink), rarely spotted with red-brown. Inner corona lobes adpressed to backs of anthers and not rising steeply towards centre.

The second variety of *P. cornutus* is of restricted distribution in the mountains east of the southern Namib Desert between Rosh Pinah and Aus in Namibia and apparently does not extend east of the Konkiep River. The flowers in this area are mostly a little different from those found elsewhere, though intermediates have been seen. The corolla lobes are broader and do not taper as gradually to their tips. They often spread out more fully so that the corolla is flatter than in typical *P. cornutus*. Inside, the corolla is often uniformly coloured, usually cream or yellow but occasionally suffused with pink. Plants have been found where it is also spotted, as was the case in the original collection by Ernst FT. Rusch. As a consequence of the

slightly broader, less slender lobes, flowers in most of these plants bear a strong resemblance to those of *P. geminatus* (especially *f. disparilis*). This resemblance is reinforced by the manner in which the inner corona lobes do not rise beyond the anthers as is usual in *P. cornutus*.

This element is recognised here as *P. cornutus* var. *ruschii* at varietal level since plants ascribable to var. *cornutus* have been found very close by and might even occur together with it.

Var. *ruschii* was discovered by Ernst FT. Rusch at Pockenbank, south of Aus. This collection was illustrated in White & Sloane (1937) and described there by G.C. Nel.



Fig. 12.60. *P. cornutus* var. *ruschii*, PVB 3910, east of Rosh Pinah, Namibia, flowers here slightly suffused with pink.



Fig. 12.61. *P. cornutus* var. *ruschii*, PVB 3929, north of Rosh Pinah, Namibia, an unusual spotted flower.



Fig. 12.62. *P. cornutus* var. *ruschii*, PVB 7203, north-east of Witpütz, Namibia.

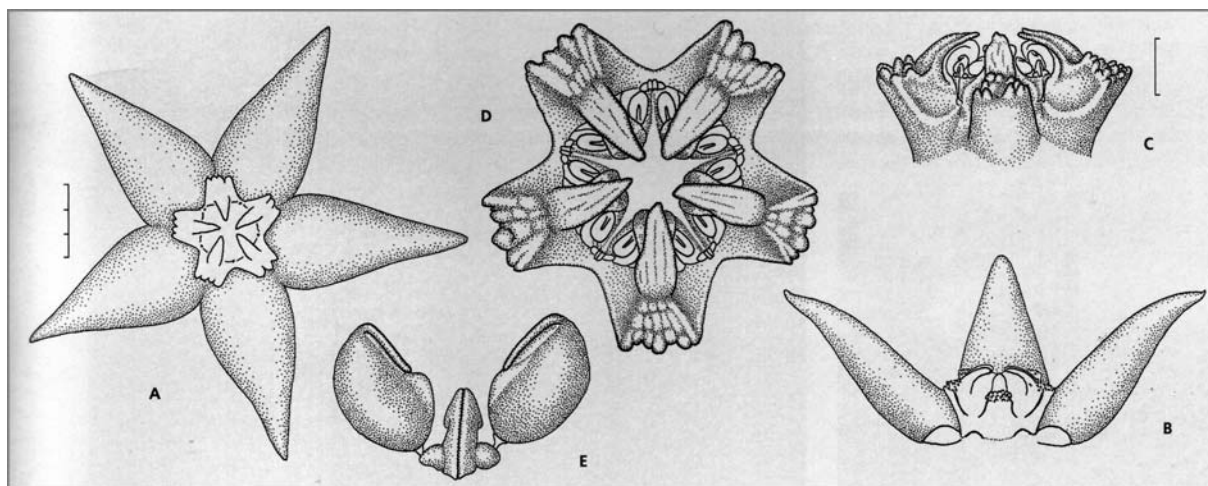


Fig. 12.63. *Piaranthus cornutus* var. *ruschii*. A, face view of flower. B, side view of dissected flower. C, side view of gynostegium. D, face view of gynostegium. E, pollinarium. Scale bars: A, B, 3 mm (at A); C, 1 mm; D, 1 mm (at A); E, 0.25 mm (at A). Drawn from: PVB 3064, Namuskluft, near Rosh Pinah, Namibia.

6. *Piранthus comptus*

Piранthus comptus N.E.Br., Hooker's Icon. Pl. 20: t. 1924B (1890).

Caralluma comptus (N.E.Br.) Schltr., J. Bot. 36: 479 (1898).

Lectotype (selected here): South Africa, Cape, Prince Albert distr., Grootfontein, Barkly 58 (K). *Piранthus comptus* var. *ciliatus* N.E.Br., Fl. Cap. 4 (1): 1023 (1909).

Type: Cape, Grootfontein, N.S. Pillans 186 (K, holo.; BOL, iso.).

Stems 10-50 mm long, 10-22 mm thick, dark grey-green, subglobose, somewhat papillate; **tubercles** with apical deltid leaf-rudiment ± 1 mm long. **Pedice** 5-15 mm long, 1-2 mm thick. **Corolla** 14-17 (-24) mm diam., rotate; inside white to cream (light brown) usually boldly spotted with red to red-brown (more rarely transversely banded with these darker colours), covered with slightly swollen acute papillae 0.4-1.0 mm long; **tube** $\pm$ absent but sometimes shallowly plate-like with slight annulus-like thickening of **corolla** at base of lobes; **lobes** 6-10 mm long, 3-5 mm broad at base, spreading, lanceolate, acute, margins somewhat recurved, with vibratile clavate cilia up to 1 mm long near base. **Corona** 2-6-3-2 mm tall, 3.5-4.8 mm broad, yellow with upper surface reddish; **outer lobes** forming narrow platform beneath guide-rails and tuberculate sometimes rounded crest 0.8-1.5 mm wide behind inner lobes; **inner lobes** 1.0-1.5 mm long, ± 0.6 mm broad, adpressed to backs of anthers and often slightly exceeding them, linear to subulate, acute to emarginate.

Distribution and habitat

Piранthus comptus occurs in the southern portion of the Great Karoo and is mostly found in the area between Beaufort West and Nelspoort in the north, Merweville and Matjiesfontein in the west and Prince Albert and Rietbron in the east. There are a few isolated collections from around Graaff-Reinet and Cradock.

Plants are frequently encountered in gravelly, flattish spots on or between low, stony, shale ridges and are often associated with shrubs of *Rhigozum obovatum* or *Lycium*.



Fig. 12.65. *P. comptus*, PVB 3665, Karoo National Park, Beaufort West, an especially dark-flowered plant.

Diagnostic features and relationships

In the region mentioned above in the Great Karoo, *P. comptus* is distinctive and easily recognised. Plants form small mounds of compact stems with relatively small flowers which are invariably less than 20 mm broad. The inside of the corolla is covered with fairly long papillae which reach 1 mm in length. It has a white background with bold, usually nearly circular, bright red to red-brown spots which occasionally lengthen into broken, transverse bands towards the bases of the lobes.

However, to the north of this region and in the south, this distinctness becomes blurred. In some populations north of Beaufort West and near Britstown, the flowers are to some extent intermediate with *P. cornutus*. They are somewhat on the large side for *P. comptus* (23-25 mm in diameter), with narrower corolla lobes as in *P. cornutus* but have bold spots and relatively long papillae on the interior as in *P. comptus*. Those around Britstown also have the erect tips of the inner corona lobes which are typical of *P. cornutus*. Similarly, south of Laingsburg in the vicinity of Rooinek Pass (in the grid squares 3320 BB, BD, 3321 AC), some plants have been collected with distinctly broader corolla lobes and shorter papillae. These still have, however, the characteristic spots on a white background of *P. comptus*. *P. geminatus* subsp. *geminatus* is recorded from the same area (3320 BB, BC) and there appears to be intergradation between

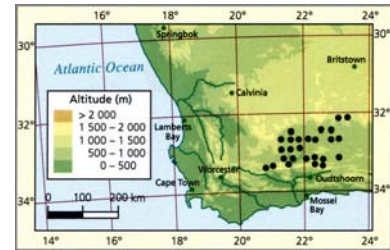


Fig. 12.64. Distribution of *Piранthus comptus*.

the two here.

It seems, therefore, that the discreteness of *P. comptus* as a species is open to question. Meve mentioned that the papillae on the inside of the corolla are the longest in the genus (and reach 1 mm long). However, according to his Table 4 (Meve 1994: 69), these papillae also reach 1 mm long in *P. cornutus*. Thus, even though they may more frequently attain this length in *P. comptus*, they cannot always be used to separate the two. In the case of *P. geminatus*, he observed that *P. comptus* exhibits 'far-reaching overlaps of habitat' with *P. geminatus*, although he also noted that *P. comptus* is 'ecologically very well characterised'. This appears to be contradictory and the existence of some intermediates suggests that these statements might not be correct. He also mentioned (probably as evidence that it is a distinct species) that *P. comptus* is sympatric with *P. geminatus* subsp. *decorus*. However, amongst the records that he cited,



Fig. 12.66. *P. comptus*, PVB 3082, east of Prince Albert, flower with typical round spots and fairly long papillae.



Fig. 12.67. *P. comptus*, PVB 3060, south of Laingsburg, possibly intermediate with *P. geminatus*.

P. comptus is not found in any quarter-degree square together with subsp. *decorus*. Therefore this statement is not corroborated by his own data and it is unclear on what it was based.

In the present account *P. comptus* is left as a distinct species as its relationships with '*cornutus*' have not yet been adequately elucidated, nor is it clear how it is related to the '*geminatus*' complex.

History

Piaranthus comptus was first recorded by Dickson and Henry Barkly before 1874. These collections were all made on the farm Gootfontein near Prince Albert. Brown (1890) cited three syntypes and one of these has been selected here as the lectotype.



Fig. 12.68. *P. comptus*, PVB 6392, north of Beaufort West.



Fig. 12.69. *P. comptus*, PVB 6392, north of Beaufort West. In this plant the flowers are somewhat like in *P. cornutus*.

7. *Piaranthus parvulus*

Piaranthus parvulus N.E.Br., *Fl. Cap.* 4 (1): 1023 (1909).

Type: South Africa, Cape, Matjiesfontein, N.S. Pillans 130 (K, holo.; BOL, GRA, iso.).

Stems 15-50 (-90) mm long, 10-20 mm thick, subglobose, green to dark grey-green, smooth; **tubercles** with apical deltoid leaf-rudiment 0.5-1.0 mm long. **Inflorescences** bearing 1-10 flowers opening in $\pm$ rapid succession on gradually lengthening peduncle up to 15 mm long; **pedicel** 4-25 mm long, $\pm$ 1 mm thick; **sepals** 1-2 mm long, 1 mm broad at base. **Corolla** 6-13 mm diam., $\pm$ campanulate to rotate; inside pale to bright yellow sometimes faintly spotted or transversely barred with red-brown, covered with fine papillae (< 0.2 mm long); **tube** $\pm$ absent; **lobes** 3-7 mm long, 1.8-2.2 (-3.0) mm broad at base, ascending often with recurved tips, lanceolate, acute, with margins slightly recurved, eciliate. **Corona** 2.0-3.2 mm tall, 2.0-3.5 mm broad, yellow; **outer lobes** forming narrow platform beneath guide-rails and rounded-verrucose to tuberculate ascending to spreading crest $\pm$ 1 mm wide behind inner lobes; **inner lobes** 1.0-1.8 mm long, 0.3-0.6 mm broad, adpressed to backs of anthers for lower half of anthers then erect and often with recurved apices, subulate to narrowly deltoid to linear, acute to obtuse or truncate-emarginate, margins sometimes folded back so that channelled above.

Distribution and habitat

Piaranthus parvulus occurs in the southern portion of the Ceres Karoo, from around the foot of Skittery Kloof southwards to Matjiesfontein on the western side and on the eastern side in the area below Verlatekloof. In the Great Karoo it is found from Matjiesfontein eastwards to Laingsburg and north of Laingsburg in the so-called Moordenaarskaroo. Meve (1994) recorded a single collection from Oudtshoorn in the Little Karoo but this has not been verified. As it is considered to be doubtful, it was excluded from the distribution map.

This species is especially associated with tillites of the Dwyka Series. It is frequently found growing under small, spiny *Ruschia* bushes. South of Laingsburg, it will often be encountered where some Witteberg quartzite rubble overlays the tillites, under shrublets of *Pteronia pallens*.

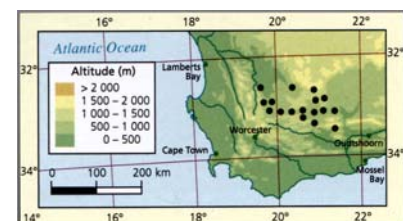


Fig. 12.70. Distribution of *Piaranthus parvulus*.

PIARANTHUS PARVULUS



Fig. 12.71. *P. parvulus*, PVB 6269, north-west of Matjiesfontein.

Diagnostic features and relationships

Piaranthus parvulus is often easy to recognise even when not in flower by the numerous inflorescences towards the apices of the stems which form slightly knobby peduncles. Flowers are usually produced in large numbers, each inflorescence often bearing as many as 10 of them in various stages of development. The flowers themselves are distinctive for their small size. They may reach 13 mm in diameter but are often only 10 mm across or even smaller (down to 6 mm), with the lobes mostly less than 2.2 mm broad (occasionally up to 3 mm). Like the corolla, most of the other parts of the flower are also smaller. So, for example, the corona is usually less than 3 mm across (where in most of the others it is generally over 4.5 mm in diameter) and the anthers are smaller. As a consequence, the pollinia are usually about half the size of those in the other species (at $\pm$ 0.23–0.35 mm long, where they are normally 0.5–0.7 mm long). However, it should be noted here that even this feature is variable and some specimens in the Ceres Karoo (e.g. *KG 100/73* (NBG) from Tulpfontein) also have considerably larger pollinia (up to 0.42 mm long).

One of the distinctive features of *P. parvulus* is the ascending to erect orientation of the inner corona lobes. This is sometimes found in



Fig. 12.72. *P. parvulus*, PVB 6269, north-west of Matjiesfontein.

P. punctatus as well and nearly always in *P. cornutus* but is absent in the '*geminatus*' complex. They are usually only adpressed to the anthers in the lower half (of the anthers) after which they rise, sometimes straight up above the anthers, occasionally with recurved tips, while on other occasions they may be somewhat convoluted towards the centre. As is usual, they are very variable in shape, varying from slender and more or less linear to relatively broad and dorsally channelled.

Piaranthus parvulus occurs together with *P. punctatus* in the southern Ceres Karoo around the foot of Skittery Kloof, with *P. comptus* around Laingsburg and together with *P. geminatus* subsp. *decorus* on the south-eastern side of the Ceres Karoo along the foot of the escarpment. For the most part it appears that the small

pollinia prevent any hybridisation from taking place (Meve 1994: 65). The only evidence for any intergradation, in this case with *P. comptus*, is found in some specimens from around the Rooinek Pass south of Laingsburg (*Bayer 2713* (NBG)). These plants had fairly small flowers (13 mm in diameter), large outer coronal crests beneath the inner lobes and inner lobes adpressed to the anthers for their whole length, ascending but not erect.

History

Piaranthus parvulus was discovered in 1903 by N.S. Pillans one mile east of Matjiesfontein. This lies almost in the centre of its area of distribution and it still occurs there in reasonable quantities.

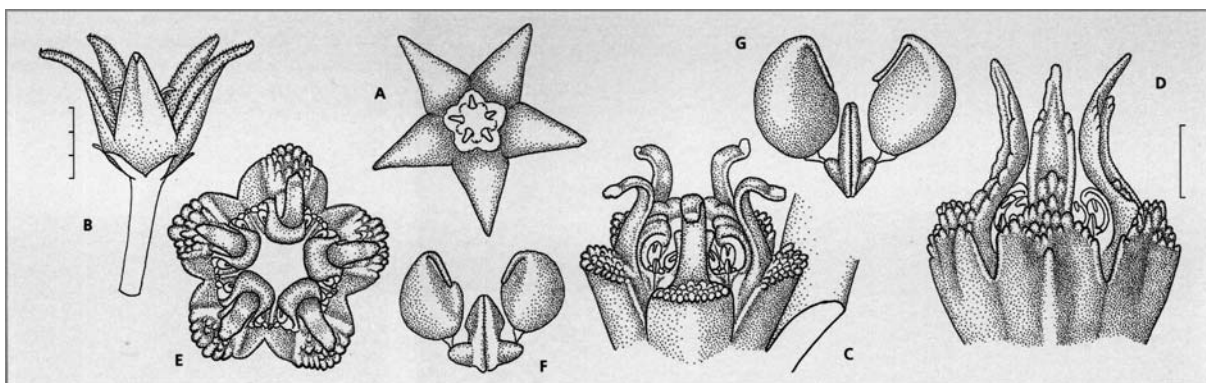
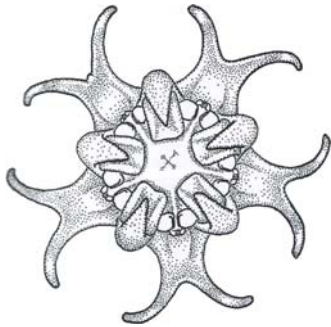


Fig. 12.73. *Piaranthus parvulus*. A, face view of flower. B, side view of flower. C, D, side view of gynostegium. E, face view of gynostegium. F, G, pollinarium. Scale bars: A, B, 3 mm (at B); C-E, 1 mm (at D); F, G, 0.25 mm (at D). Drawn from: A-C, E, F, PVB 3102, Klipfontein, north-east of Laingsburg; D, G, *Bayer sub KG 100/73*, Tulpfontein, 40 km north of Karooport.

13. Quaqua



Quaqua was published on 5 July 1879 by N.E. Brown for the single species *Q. hottentotorum*. He mentioned on this occasion that he suspected that *Stapelia pruinosa*, *S. parviflora* and *S. arida*, which were all described by Masson, might belong to the same genus. However, in 1879 they were all still known only

from Masson's figures and so the lack of accurate information and the absence of any freshly collected material that he could have examined made him unsure of this. He also found that the habit of his new species was very like that of '*Boucerosia incarnata*' but that its corona and 'especially the remarkable form of the pollinia...[were] very different from the pollinia of any other stapeliad that I have examined' and that these entitled it to the rank of genus. At this stage he appears to have been particularly impressed by pollinia in different genera, about which he expounded at length (Brown 1879). However, he was soon to lose interest in these structures and abandoned *Quaqua* later, placing *Q. hottentotorum* in *Caralluma* without any comment (Brown 1890). It is possibly noteworthy that on this occasion he mentioned that the corona of '*Caralluma dependens*' is exactly the same as that in the Indian species *Caralluma adscendens* and this might explain partly why he abandoned any further attempt to subdivide *Caralluma*. Nevertheless it is interesting that, in Brown (1890), all the species known to him

which are now in *Quaqua* are discussed under three consecutive plates so that Brown's understanding of the relationships of these species is reflected in their present position in a single genus. The name *Quaqua* is derived from a Hottentot word *Qua-qua* which appears to have been used in some parts of Namaqualand for *Q. incarnata* subsp. *hottentotorum*. At present, the genus contains 19 species (Bruyns 1999a).

Quaqua N.E. Brown, Gard. Chron. N.S. 12: 8 (1879).
Type: *Quaqua hottentotorum* N.E.Br. [= *Quaqua incarnata* (L.) Bruyns subsp. *hottentotorum* (N.E.Br.) Bruyns].

Sarcophagophilus Dinter, Feddes Repert. Spec. Nov. Regni Veg. 19:156 (1923).

Type: *Sarcophagophilus winklerianus* Dinter [= *Quaqua mammillaris* (L.) Bruyns].

Sometimes spiky non-rhizomatous succulent forming subshrub to shrub up to 900 mm diam. **Stems** 50-500 mm long, 15-40 mm thick, erect to decumbent or spreading, fleshy and hard, glabrous, grey-green to purplish green often mottled with darker purple; **tubercles** 1-10 mm

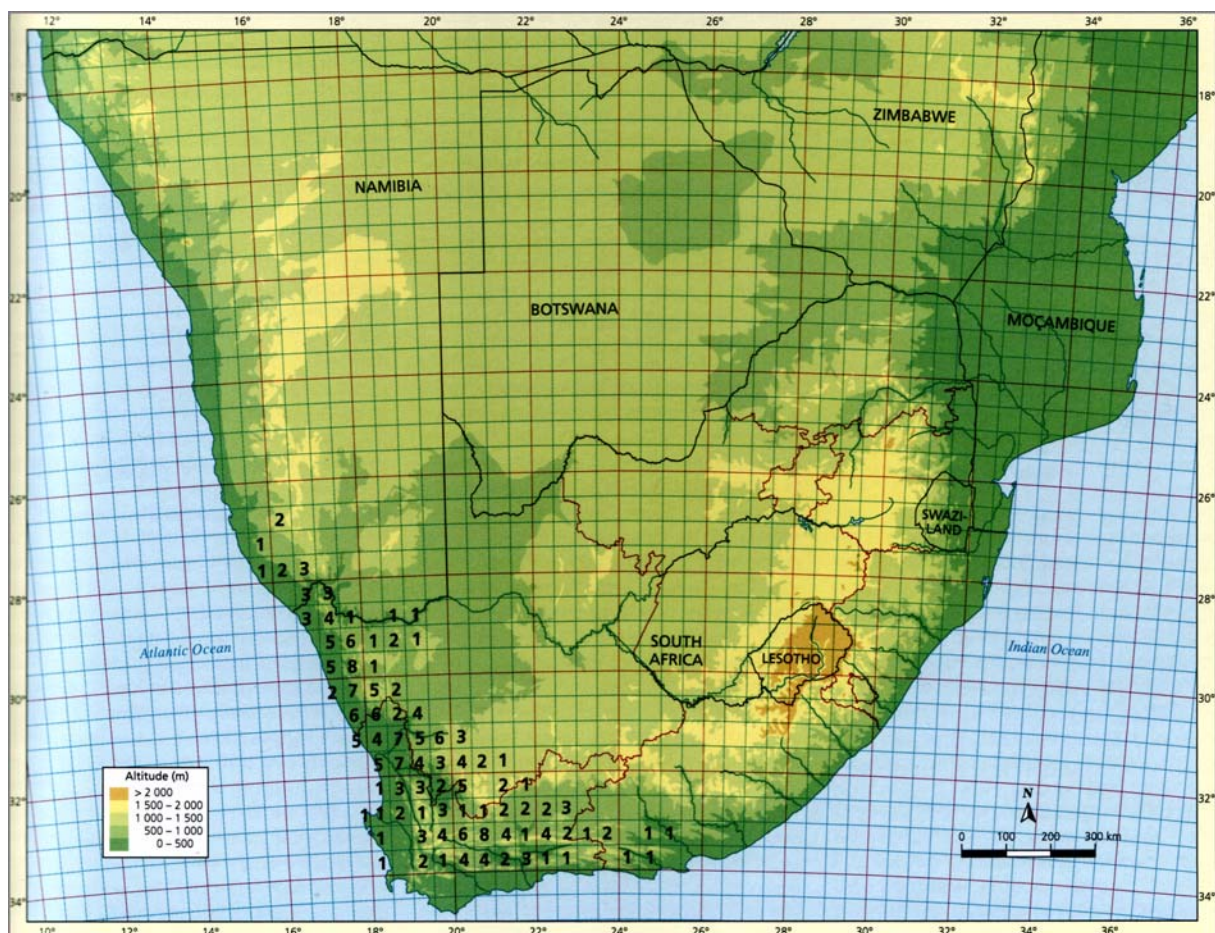


Fig. 13.1. Patterns of diversity in *Quaqua*, showing the number of species recorded to date in each half-degree square.

QUAQUA

long, conical to obtuse, spreading, sometimes laterally flattened, joined into 4 (rarely 5 or 6) angles along stem, each tipped with a hardened yellow-brown tooth sometimes flanked by 2 stipular denticles. **Inflorescences** glabrous, 1-20 per stem, solitary or often in vertical series in grooves on opposite sides of stem, arising mainly in upper part of stem between angles, each bearing 1-30 flowers and forming peduncular patches with many narrowly deltoid bracts < 1.5 mm long often with lateral teeth near base; **pedicel** 1-15 mm long, 0.5-2.0 mm thick, ascending to descending; **sepals** 1.5-1.0 mm long, $\pm$ 0.5-1.0 mm broad at base, lanceolate, acute. **Corolla** 7-25 mm diam., rotate to campanulate, mostly deeply lobed; outside glabrous and smooth; inside frequently with obtuse conical papillae each tipped with an apical bristle (especially around mouth of tube and bases of lobes), glabrous or rarely with fine crinkled or cylindrical hairs; **tube** shallow to cupular or conical, up to 5 mm deep; **lobes** (2-) 3-15 mm long, ascending to spreading or reflexed, ovate-lanceolate to linear, acute to obtuse, usually folded longitudinally so that upper surface convex, margins sometimes ciliate. **Corona** 1.5-4.5 mm diam., consisting of 2 series arising on staminal tube and partly intergrown, glabrous (occasionally bases of inner corona lobes slightly hispid), often raised on short obtusely pentagonal stipe; **outer lobes** 0.5-2.0 mm long, deeply to shallowly bifid, often consisting of small erect teeth between inner corona lobes but sometimes $\pm$ linear, ascending-spreading and only bifid at apex, often laterally fused with bases of inner lobes and sometimes forming small pouch, dorsiventrally flattened and often channelled down inner surface; **inner lobes** 0.3-2.0 mm long, adpressed to backs of anthers for most of anthers' length, sometimes exceeding them and rising in centre in small column, usually dorsiventrally flattened, often with short obtuse dorsal process near base nearly confluent with or fused to outer lobes. **Anthers** horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** ellipsoidal, longer than broad to broader than long, insertion-crest exactly along outer edge, caudicle attached with small $\pm$ circular pad to ventral surface. **Follicles** erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

The species of *Quaqua* are usually quite easily recognised as belonging to this genus. They mostly have relatively stout, firm, 4- or 5-angled stems bearing conical (to laterally flattened) tubercles each of which is tipped with a hard, acute, yellow to brown, spike-like tip (fig. 17 C, D). Although neither as sharp nor as attenuated as in *Hoodia*, these spikes (especially in *Q. mammillaris*) are not to be trifled with. In a few, such as *Q. linearis* (fig. 19 H), *Q. pruinosa* and *Q. ramosa*, these tubercles are much reduced to a short, blunt tooth or even entirely absent (especially in *Q. ramosa*, fig. 17 E). Many of them form spreading clumps but several (particularly *Q. mammillaris*, *Q. pillansii* (fig. 13) and *Q. ramosa*) often become substantial shrubs up to 0.6 m in diameter and height, a size rivaled only by some *Hoodia* and some of the large *Caralluma*s in East Africa and Arabia.

These larger plants frequently root only by the central (primary) stem and, although cuttings may be persuaded to root, this does not take place naturally.

Quaqua is distinctive among the stapeliads

in southern Africa for the large numbers of inflorescences (fig. 22 D) that are produced and a typical stem may have anything up to 20 of these. In most species new inflorescences are almost immediately active. Consequently the majority of flowers is found in the upper half of the stems although older inflorescences may still give rise to flowers and this leads to odd flowers being found at practically any height on the stem. The only regular exception to this is in *Q. arenicola*, where the flowers may also be found at any height but most of them are towards the base. In this case the development of the inflorescences is inhibited until they are well below the apex of the stem so that they bear flowers most vigorously when they are towards the base of the stem.

In most stapeliads the production of inflorescences disrupts the vertical rows of tubercles along the stem. Although this is also true sometimes in *Quaqua*, it will mostly be observed here that the tubercles retain their arrangement into rows past the inflorescences. It will be noticed too that the inflorescences frequently are ordered distichously into vertical sequences. These sequences usually continue for a while on two opposite sides of the stem, then change to two vertical distichous sequences in the other two opposite grooves.

In general in *Quaqua* the inflorescence tends to remain flat against the stem, forming a 'peduncular patch' rather than a peduncle of any significant length. With time such a peduncle becomes a slightly raised mound of old scars from the numerous pedicels and plenty of small, lanceolate bracts that are present. There is substantial variation in the number of flowers per inflorescence and the rate at which they open. In some, such as *Q. acutiloba*, *Q. cincta*, *Q. inversa* and *Q. parviflora*, each inflorescence bears only 1-3 flowers which open in gradual succession. The opposite extreme is found in *Q. arenicola*, *Q. armata*, *Q. mammillaris*, *Q. multiflora*, *Q. pillansii* and *Q. ramosa*, where the flowers arise in clusters (of up to 15 but as many as 30 in *Q. multiflora*) and all open more or less simultaneously on each inflorescence.

Flowers in *Quaqua* are generally small and, apart from some species of Sect. *Quaqua*, are mostly between 7 and 15 mm in diameter. In Sect. *Quaqua* they may be up to 27 mm in diameter, although they rarely spread out fully. There is a considerable variety of colours and some of the small-flowered species (especially *Q. inversa*) have particularly beautiful flowers. Several of the larger-flowered ones have papillate, dark maroon or brown to blackish flowers and these have the usual foul, excrement-like to urine-like stench associated with dark-flowered stapeliads generally. There are a few (such as *Q. aurea*, some forms of *Q. incarnata* and *Q. pruinosa*) which emit more pleasant, fruity

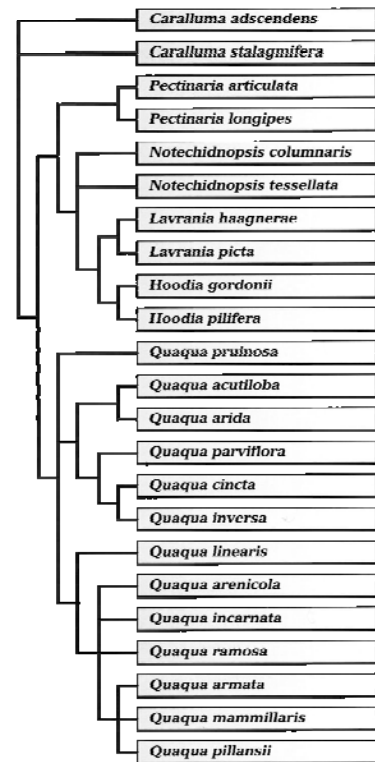


Fig. 13.2. Simplified cladogram derived from morphological characters showing the possible relationships among the species of *Quaqua* (Bruyns 1999a).

to honey-like odours; in *Q. incarnata* subsp. *hottentotorum* these may even be deliciously sweet. These sweeter odours are usually quite fleetingly detectable.

The corona in *Quaqua* is not particularly distinctive but perhaps one of the most interesting things to observe about it is the remarkable similarity between the corona in *Q. parviflora* (and a few others), *Caralluma adscendens*, some species of *Rhytidocaulon* and even certain species of *Brachystelma*. This similarity is not coincidental and hints at the close relationship that has been found to exist between many of these genera (Bruyns 2000a).

A final distinctive characteristic of *Quaqua* is to be found in the seed and seedlings. The follicles are erect, slenderly obclavate and longitudinally striped and the horns diverge from one another at between 30-60°. They contain many pear-shaped seeds 4-6 mm long and the seeds are distinctive in that their entire

surface is papillate and uniformly coloured, whereas most stapeliad seed has a differently coloured, more or less smooth margin. The seedlings have the usual broadly to narrowly wedge-shaped hypocotyl but have very small and practically undifferentiated cotyledons.

Quaqua has a relatively compact distribution in the south-western corner of southern Africa (fig. 13.1). The species are mainly found within the region receiving winter-rainfall, with a few venturing slightly beyond the western edge of the arid all-year rainfall zone: they are found from Aus in southern Namibia southwards to near the Cape Peninsula (but not on it) and eastwards from Worcester to the western edge of the Suurberg (north of Kirkwood). There are outliers in the arid Warmbad-Pofadder area of southern Namibia and Bushmanland. Apart from a few rogue collections in the Warmbad-Pofadder area and the Fraserburg district (in the western Cape), their distribution fits closely into the 'Succulent Karoo Region' (Jürgens 1991) and the distributions of *Quaqua* and *Tromotriche* are almost identical. To a large extent the eastern boundary of the distribution of *Quaqua* coincides with the areas of high concentrations of spiny species of *Ruschia*, and *Quaqua* becomes rare to the east of areas where these plants dominate. As for *Tromotriche*, alongside rainfall patterns, one of the most decisive influences appears to be the edge of the Karoo dolerite 'plate' and only *Q. acutiloba*, *Q. arenicola* subsp. *pilifera* and *Q. arida* appear to have tolerance for soils derived from this rock type. Unlike many other stapeliad genera (but similarly to *Stapelia*), *Quaqua* has been quite successful in colonising the nutrient-poor soils of the sandstone mountains of the Western Cape and there are two species that are found only in this soil type. This is also the case for *Tromotriche*, where there are two such species.

There are several areas where the number of species of *Quaqua* rises above five per half-degree square and a maximum of eight species is reached in the mountains to the south of Springbok in Namaqualand and also in the area around Matjiesfontein in the south-western corner of the Great Karoo. Seven species have also been recorded from the Knersvlakte between Vredendal and Bitterfontein. There are several species of *Quaqua* with restricted distributions and these are all found in Namaqualand between Springbok and Vanrhynsdorp.

The larger species of *Quaqua* (especially *Q. mammillaris* and *Q. pillansii*) grow fully in the open in flats (sometimes even in sand on the west coast in the case of *Q. mammillaris*) or on stony slopes. Most plants of the other species will be found under bushes on flats to slopes or even on the summits of hills. Several species (for example *Q. acutiloba* and *Q. arida*) are often associated with colony-forming spiny and non-spiny species of *Ruschia*, growing around the bases of the stems of such a shrub.

Key to the sections

1. Stems tapering to apex, corolla face lightly rugulose (not raised into discrete papillae), covered with fine crinkled hairs I. Sect. *Pseudorhytidocaulon*
1. Stems not tapering, corolla face smooth or papillate, glabrous or with rigid cylindrical hairs 2.
2. Corolla uniformly yellow, cream or white within (sometimes suffused with pale pink) III. Sect. *Quaqua*
2. Corolla lobes purple to dark purple or mottled with purple, brown or red 3.
3. Corolla lobes longitudinally folded along middle so as to be keeled on upper surface, pedicel > 1.5 mm thick III. Sect. *Quaqua*
3. Corolla lobes not folded longitudinally (without keel), pedicel at most 1 mm thick II. Sect. *Pauciflora*

I. *Quaqua* sect. *Pseudorhytidocaulon*

Quaqua sect. *Pseudorhytidocaulon* Bruyns, Bot. Jahrb. Syst. 121: 336 (1999).

Type: *Quaqua pruinosa* (Masson) Bruyns.

1. *Quaqua pruinosa*

Quaqua pruinosa (Masson) Bruyns, Bradleya 1: 74 (1983).

Stapelia pruinosa Masson, Stap. Nov.: 24, t. 41 (1798).
Tromotriche pruinosa (Masson) Haw., Syn. PL Succ.: 37 (1812).

Caralluma pruinosa (Masson) N.E.Br., Gard. Chron. Ser. 3, 12: 370 (1892).

Type: South Africa, Cape, Namaqualand, Masson (missing).

Lectotype: Masson, Stap. Nov.: t. 41.

Caralluma pruinosa var. *nigra* C.A.Lückh. in A.C. White & B. Sloane, Stap., ed. 2, 3: 1144 (1937).

Type: Cape, Namaqualand, Van Heerde sub Lückhoff 203A (missing).

Lectotype: White and Sloane, Stap., ed. 2, 1: fig. 259.

Diffuse succulent shrublet branching well above ground level from a single centrally rooted stem. **Stems** 100-500 mm long, 10-15 (-20) mm thick, erect then spreading horizontally and somewhat tapering towards apex, greyish green to dark purple-grey or almost black especially on young growth; **tubercles** < 2 mm long, obtuse and very obscure, joined into 4 (rarely 5) obtuse and obscure angles along stem, each bearing a minute hard-tipped tooth in the middle. **Inflorescences** of 1-3 usually successively opening flowers towards tips of stems; **pedicel** 2-8 mm long, 0.5-1.0 mm thick, spreading and holding flower facing horizontally; **sepals** 1-2 mm long, ovate-acute. **Corolla** 7-13 mm diam., rotate; outside grey-green to mottled or suffused with purple-brown; inside somewhat rugulose, dark maroon (almost black) sometimes with white ring around corona, covered with fine crinkled white hairs up to 1 mm long; **tube** ± 0.5 mm long, containing less than half of column, very broadly conical to ± absent, with corolla thickened around mouth; **lobes** (2-) 3-5 mm long, 2.5-3.0 mm broad at base, deltate to deltate-lanceolate or ovate, acute, spreading. **Corona** 2 mm tall, 2.2-2.5 mm broad (usually nearly as tall as broad), black becoming reddish towards base, narrowing gradually towards base without obvious stipe; **outer lobes** with free part < 0.5

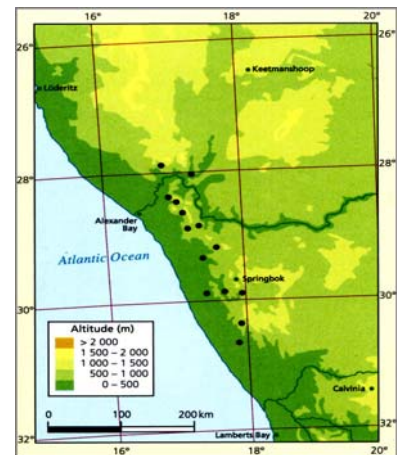


Fig. 13.3. Distribution of *Quaqua pruinosa*.

mm long, erect, shallowly bifid into small erect deltoid teeth, laterally fused for most of length with lower outer sides of inner lobes to form pouches enclosing guide-rails; **inner lobes** < 1 mm long, adpressed to backs of anthers and exceeding them, linear to deltoid with notched to obtuse apex, dorsiventrally flattened, with short ridge-like often spreading dorsal projection near base a little above outer lobes.

Distribution and habitat

Quaqua pruinosa is widely distributed in Namaqualand east of the sandveld, mainly in the hills below the escarpment, on the slopes of the escarpment itself and, more rarely, on its eastern flank. It has been recorded from near Wallekraal in the south-west and Kamieskroon in the south-east northwards into Namibia to

QUAQUA PRUINOSA

Rosh Pinah in the north-west and near the Gamkab River in the north-east.

Quaqua pruinosa is always a plant of gravelly to stony terrain and specimens usually grow inside a shrub, sometimes outgrowing it and projecting beyond it into the open. Plants are usually not particularly common.

Diagnostic features and relationships

Specimens of *Q. pruinosa* are quite remarkably distinctive in their growth form and they can usually be recognised without flowers. The plant is almost always rooted by the primary stem only, although, unlike in some species with this habit, cuttings are quite easy to root in cultivation. Although initially erect, the stems tend to spread out horizontally after some distance, often all tending to point in a particular direction, giving the plant an odd, 'windswept' appearance. This strange growth habit is usually quite obvious in large plants which project

from their protective shrub, exposing their upper parts fully to the elements and eventually looking much like old, weathered twigs. It is similar to the growth habit of many species of *Rhytidocaulon* (see Collenette 1985 for some examples). Large specimens may be anything between 0.5 m and even 0.75 m in diameter but the branching is relatively sparse and they do not form dense shrubs as do some of the other larger species. Unlike all other species in Namaqualand, *Q. pruinosa* has relatively slender, 4-angled stems that are rounded and the tubercles are obscure, each tipped by only a small, often nearly obsolete tooth. Young stems are usually very dark, often nearly black (as in *Q. linearis*) and later tend to become purple-grey with a thick covering of wax.

In *Q. pruinosa* the flowers are fairly small (usually around 10 mm across) and flat and are held slightly away from the stems. They emit a remarkably strong, lemon-like scent for a few hours after they open (usually for less than six hours) but after this passes, they are odourless.



Fig. 13.5. *Q. pruinosa*, a large specimen (about 0.5 m in diameter) in habitat north of Eksteenfontein showing the spreading habit of the branches.



Fig. 13.4. *Q. pruinosa*, PVB 6742, near Komaggas, with especially 'shaggy' flowers.

On the inside, the background colour of the corolla is usually dark maroon to almost black, although in some specimens this dark colour becomes paler maroon around the base and changes to a ring of white around the corona. In many plants this dark background colour dominates the flower so that they are not very conspicuous against the stems. Their interior is covered (in most cases) with a dense, entangled mat of fine, white, crinkled hairs which, depending on their length and denseness, can lighten the basic colour to grey and sometimes give it the 'frosted' appearance that caused Masson to name this species *Stapelia pruinosa*. This hairiness bears some resemblance also to a dense covering of mildew. Some of these hairs seem to cling to the sides of the corona, which might be slightly sticky, and in so doing they form a spiderweb-like covering of the small space around the gynostegium. The corona is mostly a dull black, contrasting quite strongly with the yellow of the anthers and pollinia and the white style-head. It consists of short outer lobes and inner lobes which just cover the anthers.

History

Quaqua pruinosa was discovered by Francis Masson in Namaqualand, probably in 1794 in the vicinity of Soebatsfontein on his last major

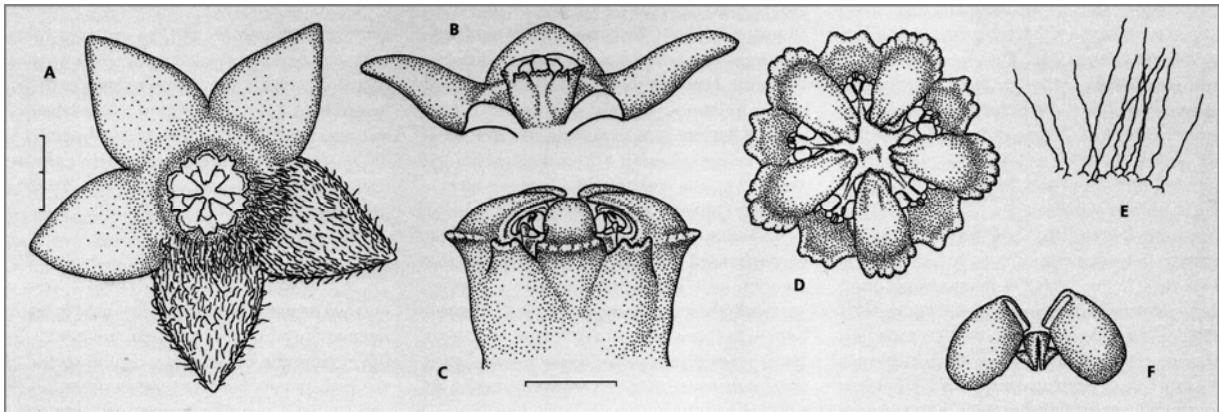


Fig. 13.6. *Quaqua pruinosa*. A, face view of flower. B, side view of dissected flower. C, side view of gynostegium. D, face view of gynostegium. E, papillae inside corolla. F, pollinarium. Scale bars: A, B, 2 mm (at A); C, D, 1 mm (at C); E, 0.5 mm (at A); F, 0.25 mm (at A). Drawn from PVB 3153, Namuskluft, near Rosh Pinah, Namibia.

expedition in the Cape before returning to London. It is remarkable that his plant survived the journey back to England, for it flowered at Kew in June of 1797. The next record seems to have been made by Edward G. Alston (see under *Hoodia alstonii*) in 1900, also somewhere in Namaqualand. Despite being known for so long, relatively few collections have been made and it has generally been regarded as very rare (Hall 1957). This is especially the case for Namibia where only two records have ever been made.



Fig. 13.7. *Q. pruinosa*, PVB 6742, near Komaggas.



Fig. 13.8. *Q. pruinosa*, PVB 7237, near Marinkasquellen along the Gamkab River, Namibia.

II. *Quaqua* sect. *Pauciflora*

Quaqua sect. *Pauciflora* Bruyns, *Bot. Jahrb. Syst.* 121: 336 (1999).

Type: *Quaqua acutiloba* (N.E.Br.) Bruyns.

Key to the species

1. Margins of corolla lobes ciliate 2.
2. Corolla with distinct tube containing corona 3.
3. Corolla lobes with yellow to green slightly thickened ends, outer corona lobes channelled down inner face only shallowly near base 8. *Q. inversa*
3. Corolla lobes inside uniformly dark purple to purple-brown and not thickened towards tips, outer corona lobes deeply channelled down whole of inner face 9. *Q. cincta*
2. Corolla tube $\pm$ absent 4.
4. Corolla lobes inside plain yellow or green-yellow above with red-pink to maroon base (marked with white), with hairs (if present) inside on darker basal area only 5.
5. Inner corona lobes with spreading to erect dorsal projection, inside of corolla glabrous, marginal cilia spatulate 8. *Q. inversa*
5. Inner corona lobes without dorsal projections, inside of corolla with hairs around base of lobes, marginal cilia not widening towards apex 7. *Q. pulchra*
4. Colour of corolla not as above, hairs (if present) scattered all over inside 6.
6. Hairs scattered all over inside of corolla 5. *Q. bayeriana*
6. Inside of corolla without hairs 4. *Q. parviflora*
1. Margins of corolla lobes eciliate 7.
7. Pedicels 3–15 mm long, holding flower well away from stem 8.
8. Inside of corolla with many stiff, erect hairs, corona bright yellow 3. *Q. arida*
8. Inside of corolla without hairs, corona yellow-green to white 6. *Q. pallens*
7. Pedicels 1–2 mm long, holding flower close to stem 2. *Q. acutiloba*

2. *Quaqua acutiloba*

Quaqua acutiloba (N.E.Br.) Bruyns, *Bradleya* 1: 44 (1983).

Caralluma acutiloba N.E.Br., *Fl. Cap.* 4 (1): 877 (1909).

Type: South Africa, Cape, Namaqualand, Templeman sub *N.S. Pillans* 8 (K, holo.; BOL, iso.).

Caralluma ortholoba Lavranos, *J. S. African Bot.* 38: 99 (1972).

Type: Cape, west of Langeberg, *Lavranos* 8227 (PRE).

Small succulent forming clump 80–300 mm diam. **Stems** 40–150 mm long, 15–20 mm thick, decumbent, green to suffused with purple or brown; **tubercles** 3–6 mm long, conical, spreading, laterally flattened towards base and joined into 4–5 angles along stem, each tipped with sharp hardened yellow tooth, without stipular denticles. **Inflorescences** of 1–3 usually successively opening flowers towards tips of stems; **pedicel** 1–2 mm long, 1 mm thick, spreading and holding flower facing horizontally; **sepals** 2.0–2.5 mm long, ovate-lanceolate, acute, adpressed to corolla. **Corolla** 8.5–13.5 mm diam., campanulate to rotate; outside green-purple; inside from uniformly purple-black to mottled with purple-black on yellow-green to uniformly yellow-green with area around gynoecium usually paler than rest, glabrous and smooth; **tube** < 1.5 mm deep and not quite containing column, very broadly and shallowly V-shaped; **lobes** 3–6 mm long, 2.5–3.5 mm broad at base, ascending to spreading, deltate. **Corona** 1.3–1.5 mm tall, 3.0–3.8 mm broad (relatively broad and

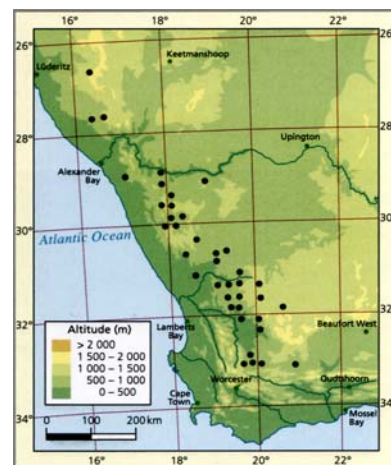


Fig. 13.9. Distribution of *Quaqua acutiloba*.

short), dark maroon to red or yellow, narrowing towards base and without stipe; **outer lobes** < 1 mm long, ascending to erect, divided deeply into 2 erect deltoid lobules, fused laterally in lower half to bases of inner lobes; **inner lobes** $\pm$ 1 mm long, adpressed to backs of anthers and exceeding them but usually not meeting in centre, linear to deltoid, obtuse to emarginate, dorsiventrally flattened, with low swollen obtuse dorsal projection just in front of outer lobes.

QUAQUA ACUTILOBA



Fig. 13.10. *Q. acutiloba*, PVB 3174, Aus, Namibia, an unusual plant, with plain yellow-green flowers.



Fig. 13.11. *Q. acutiloba*, PVB 6091, north-west of Loeriesfontein.

Distribution and habitat

A very widely distributed species, *Q. acutiloba* is found from Aus in south-western Namibia southwards into South Africa along the edge of the escarpment (both above it and below it) to a little south of Laingsburg. In general it tends to occur towards the eastern edge of the winter-rainfall zone. Nevertheless, there are several known exceptions to this, as for example around Lekkersing, north of Vanrhynsdorp, Karooport etc.

In keeping with this more easterly distribution, *Q. acutiloba* is especially associated with various gregarious species of *Ruschia*, some of them spiny like *R. spinosa* and *R. divaricata* and some spineless like *R. robusta*. Plants usually grow in gravelly and flat, low-lying areas where these species of *Ruschia* are dominant and only rarely do they grow on slopes or among rocks.

Diagnostic features and relationships

Specimens of *Q. acutiloba* form clumps up to 300 mm in diameter. Vegetatively they are not readily distinguishable from most other members of this section, although the stems are often rather irregularly 4- or 5-angled with the angles slightly spiralling and they never have the minute stipular denticles alongside the teeth on the tubercles that most of the others regularly have.

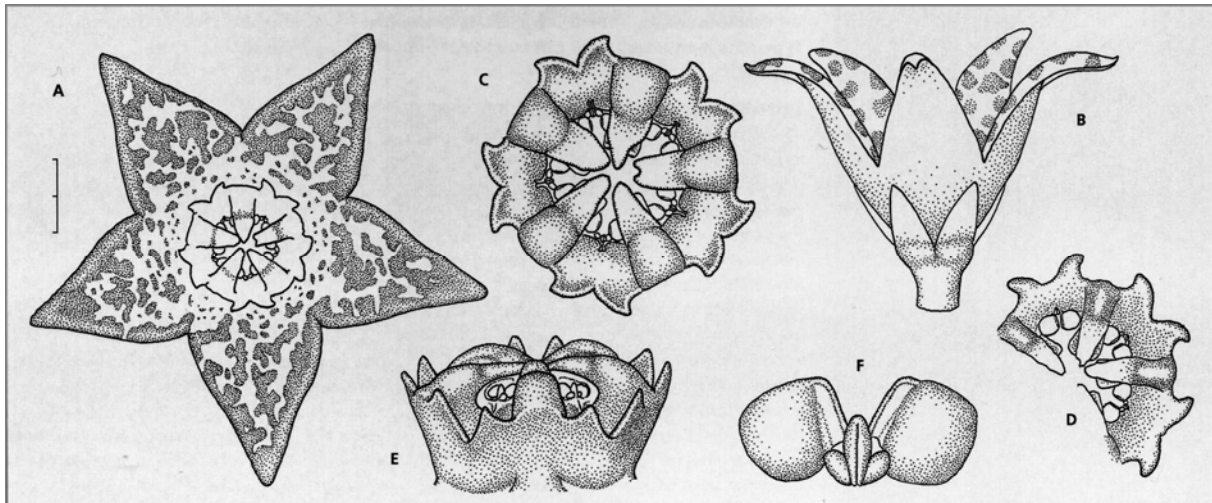


Fig. 13.12. *Quaqua acutiloba*. A, face view of flower. B, side view of flower. C, D, face view of gynostegium. E, side view of gynostegium. F, pollinarium. Scale bars: A, B, 2 mm (at A); C-E, 1 mm (at A); F, 0.25 mm (at A). Drawn from: A, C, E, F, PVB, north of Vanrhynsdorp; B, D, PVB 3174, Aus, Namibia.



Fig. 13.13. *Q. acutiloba*, PVB 6091, north-west of Loeriesfontein.



Fig. 13.14. *Q. acutiloba*, PVB 6091, north-west of Loeriesfontein.

However, *Q. acutiloba* is always easy to recognise when in flower. The buds are characteristic and unmistakable with their broadly and shortly conical shape and the very short pedicels that hold them close to the stem. The corolla is usually around 10 mm across and is practically without a tube. On the inside it is glabrous and entirely smooth. In this species the flowers are quite variable in the extent to which the lobes spread out. They are usually quite flat but occasionally they only open slightly so that the corolla has a more or less campanulate appearance. They are extremely variable in colour and may be found from dark, practically uniform purple-black to intensely or faintly spotted with purple-black on yellow-green or, on rare occasions, they are plain yellow-green (fig. 13.10).

The somewhat cup-like corona is also relatively flat and broad. The outer lobes fill the gaps between the inner lobes and each is usually divided into two very short, deltoid lobules. The inner lobes are narrow and they cover the anthers at least partly. This whole structure is usually dark red (becoming darker when the corolla is darker) but it is bright yellow when the flower is plain yellow.

History

Quaqua acutiloba was discovered somewhere in Namaqualand in 1898 by the nurseryman Robert Templeman of Rosebank, Cape Town.

3. Quaqua arida

Quaqua arida (Masson) Plowes, *Excelsa* 16: 96 (1994).

Stapelia arida Masson, *Stap. Nov.*: 21, t. 33 (1797).

Orbea ? arida (Masson) Sweet, *Hort. Brit.*, ed. 1: 277 (1826).

Piранthus aridus (Masson) G.Don, *Gen. Hist.* 4:114 (1837-8).

Caralluma arida (Masson) N.E.Br., *Gard. Chron. Ser.* 3, 12: 369 (1892).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 33.

Quaqua marlothii (N.E.Br.) Bruyns, *Bradleya* 1: 60 (1983).

Caralluma marlothii N.E.Br., *Gard. Chron. Ser.* 3, 34: 414 (1903).

Type: South Africa, Cape, Ceres division, near Zwartkops Drift, Marloth 3307 (K, holo.; PRE, iso.).

Caralluma simulans N.E.Br., *Fl. Cap.* 4 (1): 880 (1909).

Type: Cape, Prince Albert district, Marloth 4576 (missing).

Caralluma marlothii var. *viridis* E. & B.M. Lamb, *Natl. Cact. & Succ. J.* 11:77 (1956).

Type: Cape, Calvinia, Hall (missing).

Lectotype: Lamb: fig. on page 76.

Small succulent often forming dense clump 60-300 mm diam. **Stems** 50-200 mm long, 10-25 mm thick, decumbent to erect, green to purplish green or green irregularly mottled with purple; **tubercles** 3-7 mm long, conical, spreading, slightly flattened above, laterally flattened towards base and joined into 4 (rarely 5) angles along stem, each tipped with sharp hardened yellow tooth 3-5 mm long. **Inflorescences** of 1-3 usually successively opening flowers towards tips of stems; **pedicel** (1.5-) 3.0-15.0 mm long, $\pm$ 0.5 mm thick, ascending to spreading, holding

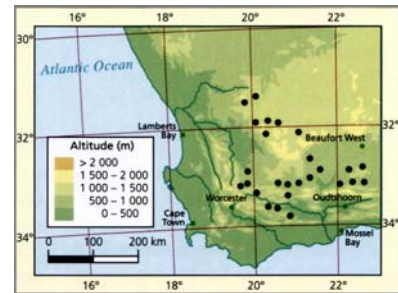


Fig. 13.15 Distribution of *Quaqua arida*.

flower facing upwards or outwards; **sepals** 1.0-1.5 mm long, $\pm$ 0.5 mm broad at base, acute, adpressed to corolla. **Corolla** 5-6 mm diam. with lobes folded back (7-10 mm diam. with lobes spread out), $\pm$ turban-shaped; outside pale green; inside on upper third of lobes pale purple-brown breaking up into short pale purple-brown transverse bars on pale greenish yellow background and becoming plain pale greenish yellow to cream around gynostegium, covered with stiff cylindrical $\pm$ erect purple to purple-red hairs reaching max. length of 1 mm and max. density in lower half of lobes; **tube** $\pm$ lacking; **lobes** 2.5-4.0 mm long, 1.5-2.0 mm broad at base, spreading with upper half recurved to touch pedicel behind corolla, ovate-lanceolate, acute, slightly thickened at tip. **Corona** $\pm$ 1.5 mm tall, 2.0-2.5 mm broad, bright yellow occasionally speckled with brown, narrowing towards base and not raised on stipe; **outer lobes** 1.0-1.5 mm long, spreading near base then erect, linear and bifid only towards apex into erect to diverging lobules, channelled down inner face, fused to inner lobes at base only; **inner lobes** $\pm$ 0.5 mm long, adpressed to backs of but not exceeding anthers, linear to narrowly deltoid, obtuse to emarginate, dorsiventrally flattened, with broad short truncate to emarginate $\pm$ erect dorsal projection near base slightly above outer lobes.



Fig. 13.16. *Q. arida*, PVB 6182, Matjiesfontein, in habitat, October 1994.

QUAQUA ARIDA

Distribution and habitat

Quaqua arida, while not rare, has a somewhat patchy distribution. Above the escarpment it is found from Loeriesfontein in the north, southwards along the Roggeveld past Sutherland to near Fraserburg. It is also present in the Ceres Karoo around Karooport from where it extends southwards to Touws River and into the Great Karoo as far north-east as Merweville and to the east as far as Prince Albert. In addition it is known on the western edge of the Little Karoo from Touws River south-eastwards to Kareevlakte and around the northern foot of the Warmwaterberg.

Specimens are often found growing inside bushes of the gregarious *Ruschia spinosa* or *R. cradockensis*. They generally occur in flat, stony or loamy areas.

Diagnostic features and relationships

Plants of *Q. arida* have quite stout, often noticeably square stems that are faintly mottled with purple. The tubercles are joined into four continuous angles along the stem and this often helps to separate it from the frequently sympatric *Q. acutiloba*, where the tubercles are much less organised into rows and the stems are usually more slender.

Flowers are produced on relatively long, slender pedicels, which are generally at least 8 mm long. A few plants have been seen (mainly in the western Little Karoo, as in PVB 6186 (BOL)) where the pedicel was between 1.5 and 3.0 mm long. Nevertheless, this character is usually adequate for recognising *Q. arida*, even if the flowers have already fallen off.

In *Q. arida* the inside of the corolla has a



Fig. 13.17. *Q. arida*, PVB 6182, Matjiesfontein, flower in the process of opening with corolla lobes spread out fully.

solid purple-brown patch in the upper third of the each lobe and irregular, pale, transverse, purple-brown bars on a greenish yellow background on most of the rest. The upper parts of the corolla lobes are bent back behind the flower to touch the pedicel more or less at the base of the sepals. As a result the dark, apical patch on each lobe is hidden from view and the tiny flower, which is usually only about 5 mm across, has a curious turban-like shape. On the inside there are many stiff, purplish hairs. These are longest and most dense around the bases of the lobes, sometimes becoming quite sparse around the middle of the lobes and then again denser towards the tips and along the margins. They are occasionally somewhat clavate.

Although the corona is small, it is bright yellow and this makes it relatively conspicuous against the generally faint colour of the corolla. The long and slender outer lobes are almost erect, channelled down the inner face and slightly split into two at their apices. The inner lobes are small and inconspicuous with a comparatively large dorsal projection nearly



Fig. 13.18. *Q. arida*, PVB 7530, foot of northern slopes of Warmwaterberg, flowers with corolla lobes fully reflexed.

in series with the outer lobes.

There are several features which indicate that, despite its more easterly distribution, this species is closely allied to the parviflora-inversa-group. The corolla has a similar pattern of colouring to some forms of *Q. parviflora*. It also has thickened tips to the corolla lobes which are found in many forms of *Q. parviflora*. Furthermore, the outer corona is fused to the inner only at its base and is channelled down the inner surface, forming very similar, nearly linear lobes as in *Q. inversa*.

History

Quaqua arida was discovered by Francis Mason. Plants that were later described as *Q. marlothii* were first recorded by Rudolf Marloth, who found his specimens in the Ceres Karoo in 1903. Brown also mentioned a collection by N.S. Pillans (Pillans 66) but this was actually collected by Marloth and may also be from the type, according to the records of the Bolus Herbarium.

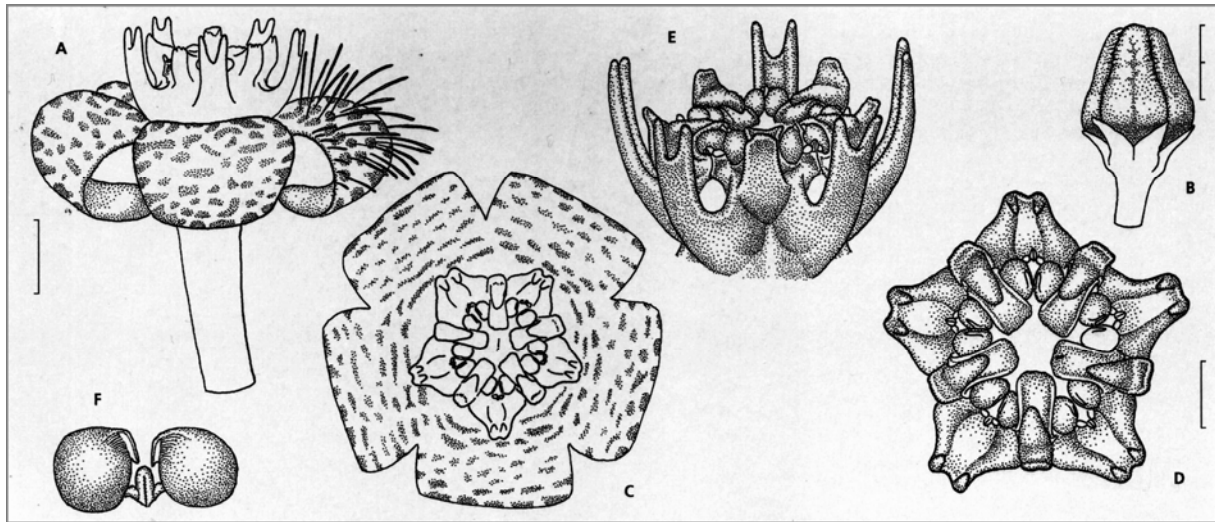


Fig. 13.19. *Quaqua arida*. A, side view of flower. B, bud. C, face view of flower. D, face view of gynostegium. E, side view of gynostegium. F, pollinarium. Scale bars: A, C, 1 mm (at A); B, 2 mm; D, E, 0.5 mm (at D); F, 0.25 mm (at A). Drawn from: C, PVB 6292, east of Middelpos; rest, Kratz, Karooport.

4. *Quaqua parviflora*

Quaqua parviflora (Masson) Bruyns, *Bradleya* 1:46(1983).

Stapelia parviflora Masson, *Stap. Nov.*: 22, t. 35 (1797).

Piarranthus parviflorus (Masson) Sweet, *Hort. Brit.*, ed. 1:278(1826).

Caralluma parviflora (Masson) N.E.Br., *Gard. Chron.* Ser. 3, 12: 370 (1892).

Type: South Africa, Cape, Namaqualand, *Masson* (missing).

Lectotype: Masson, *Stap. Nov.*: t. 35.

The *Q. parviflora*-complex consists of several allopatric forms. They occur in the winter-rainfall area in Namaqualand from Clanwilliam northwards to west of Steinkopf around Anenous and Steenbok. Some of these forms occur eastwards as far as Loeriesfontein, Calvinia and parts of the Ceres Karoo. Many of them have, at some stage or other, been recognised as separate species. However, as carefully explained in Bruyns (1999a), this does not accurately reflect their relationships, nor are they easily and reliably separable from one another and consequently they continue to be recognised here as subspecies of a single species.

In all of them the corolla, which is more or less without a tube, is variously mottled or striped (or at least bi-coloured) and the lobes are mostly adorned along their margins with fine cilia which are not noticeably clavate. The outer corona is free from the inner series right to the base and it is always bifid at least apically but sometimes very deeply into slender diverging lobules.

Small succulent forming dense to diffuse clump 60-300 mm diam. **Stems** 50-300 mm long, 8-25 mm thick, decumbent to erect, grey-green to purplish green; **tubercles** 3-6 mm long, conical, spreading to decurved, joined near base into 4 angles along stem, each tipped with sharp hardened yellow tooth 2-3 (-5) mm long, usually with stipular denticles. **Inflorescences** of 1-3 usually successively opening flowers towards tips of stems;

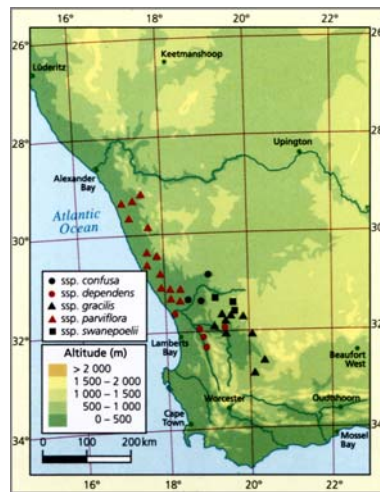


Fig. 13.20. Distribution of *Quaqua parviflora*.

pedicel 1-10 mm long, $\pm$ 0.5 mm thick, ascending to descending; **sepals** $\pm$ 2 mm long, $<$ 1 mm broad at base, ovate-lanceolate, acute, usually with recurved apices, dark green. **Corolla** 4-18 mm diam., $\pm$ rotate; inside smooth and glabrous; **tube** shallow ($<$ 1 mm deep) to lacking, containing only base of gynostegium; **lobes** 2.5-8.0 mm long, 1.5-3.5 mm broad at base, spreading to recurved, deltate to ovate-lanceolate or lanceolate, margins usually very slightly reflexed, mostly with fine flattened twisted usually dark purple cilia. **Corona** 2.2-3.7 mm diam., narrowing towards base and usually raised on obscurely pentagonal stipe up to 0.5 mm long, often with flaps of tissue projecting downwards around top of stipe; **outer lobes** 1.0-1.5 mm long, erect to spreading, deeply to shallowly bifid into often widely diverging $\pm$ cylindrical lobules, channelled down inner surface towards base, fused laterally to inner lobes at base only; **inner lobes** $<$ 1 mm long, adpressed to backs of and at most slightly exceeding anthers, dorsiventrally flattened at least at base and sometimes $\pm$ cylindrical above, with or without swollen obtuse to ridge-like dorsal projection near base.

4a. *Quaqua parviflora* subsp. *parviflora*

Caralluma virescens C.A.Luckh., 'S. A. G.' 29: 94 (1938).

Type: Cape, between Wallekraal and Soebatsfontein, *Villet sub Lückhoff* 267 (BOL).

Stems 10-20 mm thick. **Pedicel** 3-10 mm long, descending to ascending. **Corolla** 6-12 mm diam., $\pm$ rotate; inside with transverse purple-black to purple to red bars or spots on pale green, yellow or whitish background usually from base right to tips, sometimes tips solid purple to green or brown; **lobes** 2.5-6.0 mm long, 1-2 mm broad at base, spreading to slightly reflexed, lanceolate to subulate, acute, slightly thickened towards apex, margins with slender scattered cilia up to 2 mm long except in lower $\pm$ 1 mm. **Corona** 2.3-3.7 mm diam., raised on stipe up to 0.5 mm long; **outer lobes** erect, deeply bifid, lobules cylindrical and often widely spreading so as to touch at tips, dark purple to reddish becoming white towards base; **inner lobes** whitish to reddish often with a dark purple dorsal patch towards base, slenderly lanceolate, acute, dorsiventrally flattened towards base and $\pm$ cylindrical above, slightly dorsally swollen towards base but otherwise without dorsal projection.

Distribution and habitat

Subsp. *parviflora* is relatively common in Namaqualand from Moedverloor and Kotzesrus through Bitterfontein and Wallekraal to Anenous. It is mainly found among gently sloping hills and in the lower foothills of the escarpment but it does not appear to occur higher up in the Kamiesberg. My own collecting has shown that it also occurs widely in the coastal *sandveld* and specimens have been gathered at several localities between the mouth of the Groen River and the Holgat River, south of Alexander Bay, in some cases within 5 km of the shore.



Fig. 13.21. *Q. parviflora* subsp. *parviflora*, PVB 6134, west of Bitterfontein.



Fig. 13.22. *Q. parviflora* subsp. *parviflora*, PVB 7597, east of Port Nolloth.

Key to the subspecies of *Q. parviflora*

1. Outer corona lobes not exceeding height of inner corona, corolla lobes deltate 4e. subsp. *confusa*
1. Outer corona lobes exceeding height of inner corona, corolla lobes ovate-deltate to lanceolate 2.
2. Pedicel $>$ 2 mm long 3.
3. Corolla lobes not as above 4.
4. Corolla $\pm$ uniformly barred with purple against pale background, pedicel holding flower away from stem 4a. subsp. *parviflora*
4. Corolla barred with purple towards centre, with $\pm$ solid purple patch towards tip of lobe, flower usually with some lobes touching stem 4b. subsp. *dependens*
3. Corolla lobes with slight constriction near middle, thickened towards apex 4c. subsp. *gracilis*
2. Pedicel 1-2 mm long 4d. subsp. *swanepoelii*

QUAQUA PARVIFLORA

Plants usually grow on gneissic soils or firm red coastal sand. Occasionally they have been found on quartzite slopes either within bushes or in the open.

Diagnostic features and relationships

Specimens of subsp. *parviflora* found within a bush may have quite long and partly scandent stems, forming a very lax shrublet. However, if fully exposed, the stems are thick (up to 20 mm in diameter), short and erect, and they form a dense clump.

In subsp. *parviflora* the pedicel usually holds the flower well away from the stem, often in a slightly nodding attitude but also often facing upwards. The corolla lobes are normally comparatively narrow. Mostly they are barred with purplish on pale green with the bars becoming broader towards the tip of the lobe but not coalescing into a larger, dark patch at the tip. However, especially in some localities in the hills between Wallekraal and Anenous, there is much broader variation from this usual patterning to others where the dark bars coalesce towards the tip into a solid patch. In these, this darker apical patch varies from purple through brown to yellow or green.

The outer corona is usually very slender and deeply divided into fine, filiform lobules which sometimes carry a droplet of nectar near their apices. These bifid parts of the outer lobes are purple but the rest of them and the inner lobes are white, often even slightly translucent.



Fig. 13.23. *Q. parviflora* subsp. *parviflora*, PVB 1460, north-east of Wallekraal, the '*Caralluma virescens*' of Carl Lückhoff.



Fig. 13.24. *Q. parviflora* subsp. *parviflora*, PVB 1460, north-east of Wallekraal.

The inner lobes are adpressed to the anthers and they do not possess any trace of a dorsal projection.

History

Subsp. *parviflora* was discovered by Francis Masson in Namaqualand between the Olifants River and Soebatsfontein before or during 1794.



Fig. 13.25. *Q. parviflora* subsp. *parviflora*, PVB 6785, Komaggas.



Fig. 13.26. *Q. parviflora* subsp. *parviflora*, PVB 6785, Komaggas, with quite dark, brownish flowers.

White & Sloane (1937) considered it to be a 'lost species'. Nevertheless, their fig. 237, which was a photograph taken by Sidney Tapscott, shows the long pedicels and slender buds typical of this subspecies so that it was actually known to them. H. Hall also collected plants in 1954 that correspond reasonably to Masson's figure (Bruyns 1977) and today they are known from a wide area in Namaqualand.

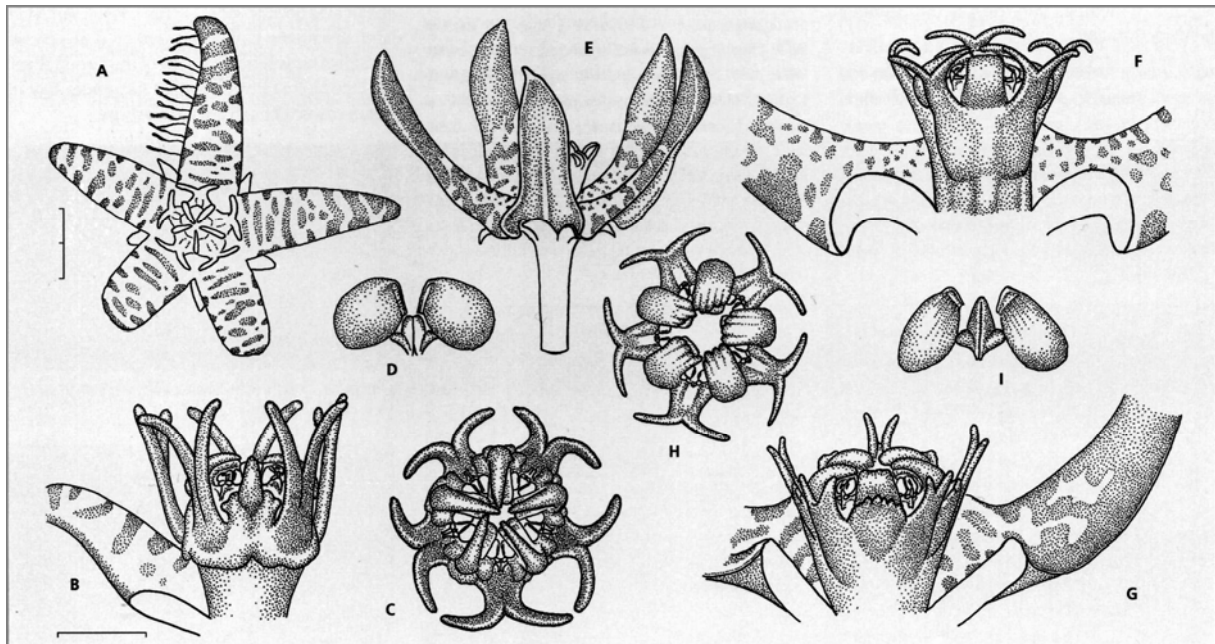


Fig. 13.27. *Quaqua parviflora* (A-D, subsp. *parviflora*; E-I, subsp. *gracilis*). A, face view of flower. B, F, G, side view of dissected flower. E, side view of flower. C, H, face view of gynostegium. D, I, pollinarium. Scale bars: A, E, 2 mm (at A); B, C, F-H, 1 mm (at B); D, I, 0.25 mm (at A). Drawn from: A-C, PVB 3889, Wildeperdehoek Pass; D, PVB 6029, Moedverloorberg; E, F, H, I, PVB 989, Gannaga Pass; G, PVB 6052, south-west of Calvinia.

4b. *Quaqua parviflora* subsp. *dependens*

Quaqua parviflora subsp. *dependens* (N.E.Br.)

Bruyns, *Bradleya* 1: 48 (1983).

Caralluma dependens N.E.Br., *Hooker's Icon. PL* 20: t. 1903B (1890).

Quaqua dependens (N.E.Br.) Plowes, *Excelsa* 16: 91 (1994).

Type: Cape, 20 miles west of Clanwilliam, *Barkly* 78 (K).

Caralluma reflexa C.A.Luckh., 'S. A. G.' 29: 94 (1938).

Type: Cape, Vanrhynsdorp division, *Villet sub Lückhoff* 268 (missing).

Lectotype: 'S.A.G.' 29: fig. after page 94.

Stems 12-20 mm thick. **Pedical** 3-5 mm long, descending and holding flower facing downwards. **Corolla** 7-11 mm diam., rotate usually with 4 lobes reflexed and other pressed against stem; inside barred with purple on pale yellow near centre to plain purple towards tips of lobes; **lobes** 2.5-4.5 mm long, 1.5-2.0 mm broad at base, spreading to reflexed, ovate-deltate to lanceolate, acute, not thickened towards apex, margins with slender cilia up to 2 mm long. **Corona** 2.5-3.0 mm diam., purple-black to brown, raised on short stipe to sessile; **outer lobes** ascending, bifid into widely diverging lobules; **inner lobes** rarely exceeding anthers, $\pm$ deltoid, dorsiventrally flattened, dorsally somewhat swollen towards base but otherwise without dorsal projection.

Distribution and habitat

Subsp. *dependens* is quite common along the southern boundary of Namaqualand. It is mainly found in the area from Citrusdal to Klawer where the vegetation is transitional from *fynbos* to karroid scrub. Here it grows mostly on drier, stony lower slopes among shrubs. It has also been recorded further east in Botterkloof, where it grows with subsp. *gracilis*. Further populations are known near the mouth



Fig. 13.28. *Q. parviflora* subsp. *dependens*, PVB 5997, Botterkloof.

of the Olifants River in the *sandveld*, growing in deep red soils covered with spiny grasses and a wide variety of succulent shrubs.

Diagnostic features and relationships

In subsp. *dependens* the flowers are variable in size and also in colour and this is especially the case in plants from around the mouth of the Olifants River. Usually the corolla is pale yellow with transverse bars of purple and a purple patch at the tips of the lobes. The flowers often have a peculiar orientation, being held facing downwards with one corolla lobe closely adpressed to the stem and fitting down the groove between the angles, while the upper two lobes are somewhat rolled back behind the flower. The pedicel can be very short indeed, approaching that in subsp. *swanepoelii* from which it is, in such cases, best separated by the narrower corolla lobes and the different colour scheme.

The corona is usually dark purple-black becoming pale towards the base, with slender



Fig. 13.29. *Q. parviflora* subsp. *dependens*, PVB 1294, west of Lutzville.

and deeply bifid outer lobes which sometimes bear a drop of liquid at their tips (as in subsp. *parviflora*). The inner lobes are without any trace of a dorsal projection.

In material from near the Olifants River mouth, the epidermis of the tubercles was found to be noticeably more papillate than that from Clanwilliam and was, in this respect, rather more similar to subsp. *parviflora*, where the surface is roughened with relatively large papillae (Bruyns 1999a). Other similarities to subsp. *parviflora* can be seen in the somewhat longer stipe on which the corona is seated with overhanging ledges of tissue from beneath the outer corona lobes. These details further serve to illustrate the closeness of these taxa.

History

Subsp. *dependens* was described by N.E. Brown from material sent to him by Henry Barkly before 1877. He also saw material from the Olifants River valley which was collected around the same time by a Mr. Hesse.

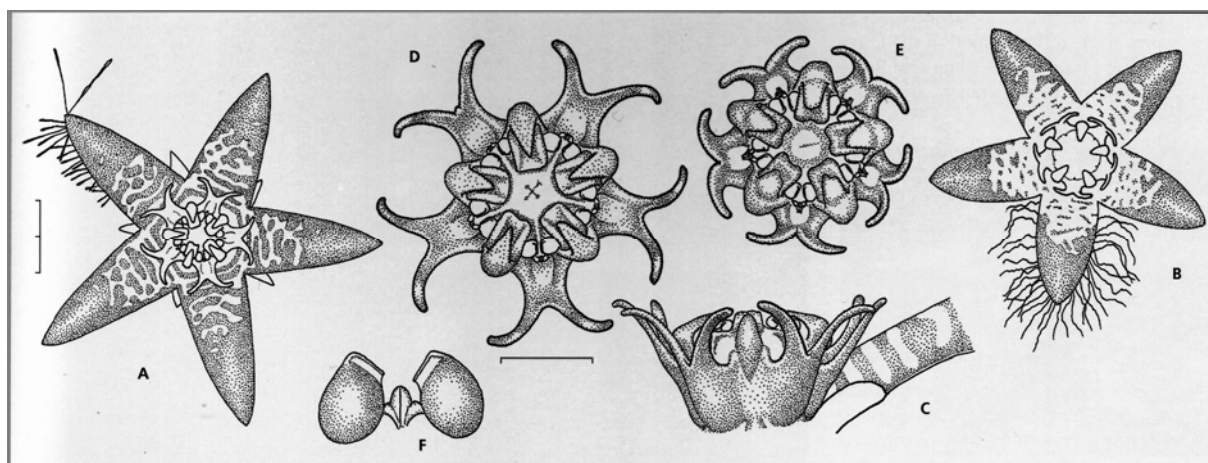


Fig. 13.30. *Quaqua parviflora* subsp. *dependens*. A, B, face view of flower. C, side view of gynostegium. D, E, face view of gynostegium. F, pollinarium. Scale bars: A, B, 2 mm at A; C-E, 1 mm (at D); F, 0.25 mm (at A). Drawn from: A, C, D, F, PVB 1294, west of Lutzville; B, E, PVB 889, Pakhuis Pass.

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4c. *Quaqua parviflora* subsp. *gracilis*

Quaqua parviflora subsp. *gracilis* (C.A.Lückh.)

Bruyns, *Bradleya* 1: 49 (1983).

Caralluma gracilis C.A.Lückh., 'S. A. G.' 28: 228 (1938).

Quaqua gracilis (C.A.Lückh.) Plowes, *Excelsa* 16: 91 (1994).

Type: Cape, between Calvinia and Pakhuis Pass, Villet sub Lückhoff 264 (missing).

Lectotype: 'S. A. G.' 28: fig. on page 228.

Caralluma ericeta Nel, *Ann. Univ. Stellenb.*, Reeks A, Wis-Natuurk. 21 (1): 15 (1943).

Type: Cape, Oudtshoorn, *Van der Merwe* (missing).

Lectotype: *Ann. Univ. Stellenb.*, Reeks A, Wis-Natuurk. 21 (1): fig. 16.

Stems 8-20 mm thick. **Pedice**l 3-5 mm long, ascending and holding flower facing upwards. **Corolla** 10-18 mm diam., $\pm$ rotate; inside whitish with purple-brown to purple-red dots (often coalescing into red-purple patch beneath differently coloured apex) from middle of lobes to centre of corolla, plain reddish brown or deep to pale yellow towards apex of lobes (rarely purple); **lobes** 5-8 mm long, 2.0-3.1 mm broad at base, spreading to ascending, lanceolate, usually with slight constriction near middle, thickened towards apex, sometimes with a few cilia up to 1 mm long along margins below thickened apex. **Corona** 2.0-3.0 mm diam., reddish brown to dark purple, mostly raised on stipe up to 0.5 mm long; **outer lobes** erect, shortly to deeply bifid into diverging to erect lobules; **inner lobes** usually $\pm$ equal to or exceeding anthers, $\pm$ rectangular, obtuse to truncate-emarginate, dorsiventrally flattened, sometimes with short erect truncate emarginate ridge-like dorsal projection.

Distribution and habitat

Subsp. *gracilis* is found along the mountainous northern to eastern edge of the Ceres Karoo, mainly along the lower slopes of the escarpment at places like Bloukrans Pass and Gannaga Pass. From Bloukrans Pass in the north it has been recorded westwards along the valley of the Doorm River to Botterkloof. In the Ceres Karoo it is also found in the south-east, some distance away from the escarpment, around the Koedoesberg.

Plants are often found inside bushes on stony slopes but in the south-eastern corner of the Ceres Karoo they may occur among colonies of the gregarious *Ruschia spinosa* and *Pteronia pallens*. It is the only member of this complex to grow with *P. pallens*.

Diagnostic features and relationships

In subsp. *gracilis* the flowers are generally held facing upwards. They have an unusual colour pattern in that towards the centre the corolla is usually white and speckled with purple-brown, with the purple-brown sometimes coalescing further out as in subsp. *swanepoelii*. The flower



Fig. 13.31. *Q. parviflora* subsp. *gracilis*, G.D. Tribe, Botterkloof.

is made considerably more striking by the fact that the tips of the lobes (which are slightly thickened) may be brown or deep to pale yellow and this then forms a strong contrast against the colours lower down.

In this respect the colour scheme differs from that in subsp. *swanepoelii*. However, in one specimen seen the lobes were initially purple mottled on white and after a day or so the tips faded to a pale yellow so that in this



Fig. 13.32. *Q. parviflora* subsp. *gracilis*, PVB 6052, south-west of Calvinia.



Fig. 13.33. *Q. parviflora* subsp. *gracilis*, PVB 6052, south-west of Calvinia.

specimen they began with the colouring of subsp. *swanepoelii* and faded to something more like subsp. *gracilis*! Other differences between the two subspecies lie in the constriction of the corolla lobes near their middle in subsp. *gracilis* (this is visible in the bud which is broad at the base then distinctly narrower above and almost beaked) and the ascending pedicel which is 3-5 mm long. However, none of these differences is constant and reliable and, in particular, plants have been collected where the lobes are not so narrow, the pedicel is ascending and the striking apical change of colour on the lobes is absent. In these cases it becomes difficult to separate this subspecies from subsp. *swanepoelii*.

The corona is raised usually on quite a long stipe and is mostly dark purple. The outer lobes are slender but only slightly bifid at the tips and the inner lobes sometimes possess a small dorsal projection.



Fig. 13.35. *Q. parviflora* subsp. *gracilis*, PVB 1167, eastern end of Biedouw Valley.



Fig. 13.34. *Q. parviflora* subsp. *gracilis*, PVB 6301, south-west of Calvinia.

History

Subsp. *gracilis* was discovered by Charles T and Elizabeth M. Villet near Botterkloof (between Calvinia and Pakhuis Pass) and independently by E. Joubert at an undisclosed locality in the Vanrhynsdorp district before 1938.



Fig. 13.36. *Q. parviflora* subsp. *gracilis*, PVB 6301, south-west of Calvinia, with flowers rather similar in colour to those of subsp. *swanepoelii*.

4d. *Quaqua parviflora* subsp. *swanepoelii*

Quaqua parviflora subsp. *swanepoelii* (Lavranos) Bruyns, *Bradleya* 1: 50 (1983).
Caralluma swanepoelii Lavranos, *J. S. African Bot.* 38: 97 (1972).
Quaqua swanepoelii (Lavranos) Plowes, *Excelsa* 16: 91 (1994).
Type: Cape, near Nieuwoudville, *Swanepoel sub* Lavranos 8371 (PRE).

Stems 15-25 mm thick. **Pedicel** 1-2 mm long, spreading and holding flower facing horizontally. **Corolla** 10-12 mm diam., rotate; inside whitish with purple to red-purple spots towards centre coalescing into dark purple or red-purple on lobes; **lobes** 3-5 mm long, 2.0-3.5 mm broad at base, spreading, ovate-deltate to ovate-lanceolate, not thickened towards apex, with cilia up to 1 mm long along margins. **Corona** 2.3-3.0 mm diam., dark purple, raised on very short stipe; **outer lobes** ascending, deeply to shallowly bifid into widely diverging lobules; **inner lobes** usually covering anthers, $\pm$ rectangular, truncate to emarginate, dorsiventrally flattened, sometimes with short erect truncate ridge-like dorsal projection.

Distribution and habitat

Subsp. *swanepoelii* is of rather restricted distribution. It is found from the dry area north-east of Nieuwoudtville to around the foot of the Hantam Mountains, north-west and north-east of Calvinia. Collections have also been made to the south and west of Calvinia.

On the plateau between Nieuwoudtville and Calvinia plants of subsp. *swanepoelii* usually grow in *Eriocephalus* or *Pteronia* shrubs. It is also known on some of the drier slopes in the valleys which dissect the area to the north and there they are often found inside shrublets of *Ruschia spinosa*.

Diagnostic features and relationships

The pedicels of subsp. *swanepoelii* are usually shorter than in any other subspecies (although the pedicels can be very short in subsp. *depen-*



Fig. 13.37. *Q. parviflora* subsp. *swanepoelii*, PVB 7970, near Klipwerf, north-east of Calvinia.

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dens) and the flowers are held flat against the stem. In the west, i.e. north-east of Nieuwoudtville, the corolla is dark purple whereas around the Hantam Mountains it tends to be more of a red-purple on the lobes and towards the centre it becomes speckled (sometimes only very slightly) with the same colour on a white to cream background.

The corona is dark and almost black with slender and deeply bifid to quite short and scarcely bifid outer lobes. The inner lobes sometimes have a small dorsal projection which takes the form of a short, toothed ridge almost in series with the outer lobes.

History

Subsp. *swanepoelii* was first recorded by R.H. Compton and others in 1950. It was ultimately described from plants collected by Jacques P. Swanepoel in about 1970.



Fig. 13.38. *Q. parviflora* subsp. *swanepoelii*, PVB 6301a, south-west of Calvinia.



Fig. 13.39. *Q. parviflora* subsp. *swanepoelii*, Nagel 215, north-west of Calvinia.

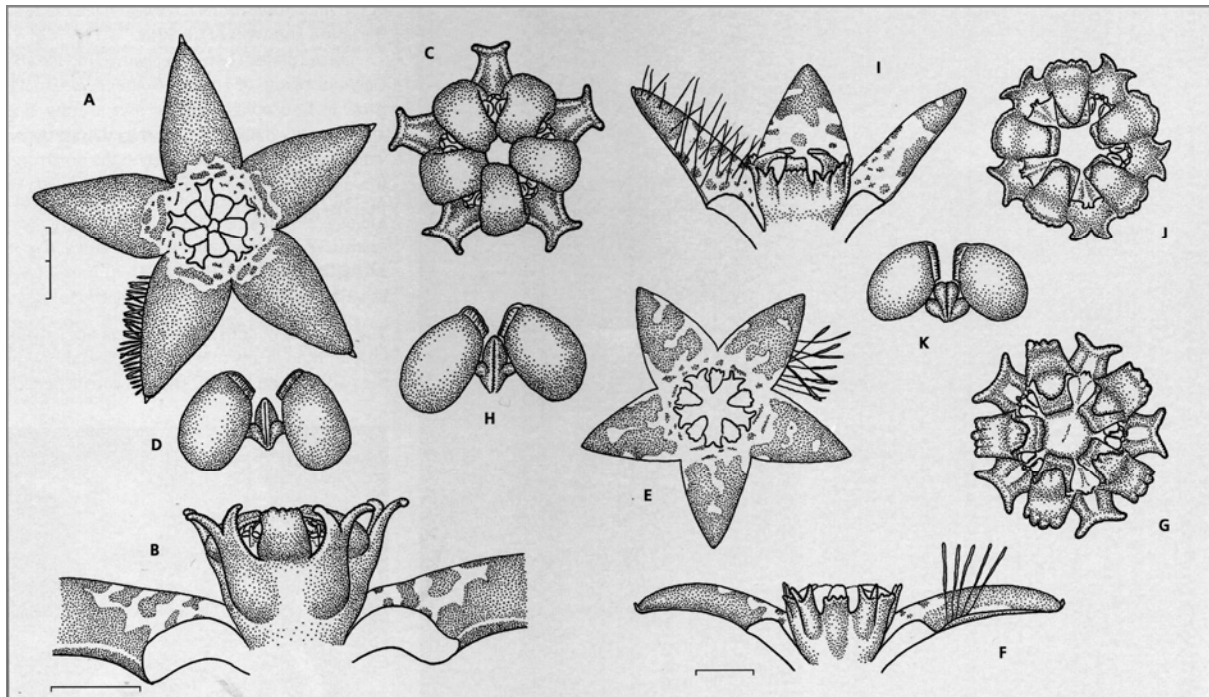


Fig. 13.40. *Quaqua parviflora* (A-D, subsp. *swanepoelii*; E-H, subsp. *confusa* and I-K, *Quaqua bayeriana*). A, E, face view of flower. B, F, I, side view of dissected flower. C, G, J, face view of gynostegium. D, H, K, pollinarium. Scale bars: A, E, 2 mm (at A); B, C, G, J, 1 mm (at B); F, I, 1 mm (at F); D, H, K, 0.25 mm (at A). Drawn from: A-D, PVB 4353, Holrivier, north-west of Calvinia; E-H, PVB 6068, south-west of Loeriesfontein; I-K, PVB 1464, Wildeperdehoek Pass.

4e. *Quaqua parviflora* subsp. *confusa*

Quaqua parviflora subsp. *confusa* (Plowes)
Bruyns, *Bot. Jahrb. Syst.* 121: 354 (1999).
Quaqua confusa Plowes, *Excefeia* 16: 92 (1994).
Type: Cape, east of Vanrhynsdorp, Grootdrif,
Plowes 3234 (SRGH).

Stems 10-20 mm thick. **Pedice**l 2-5 mm long, descending and holding flower facing downwards. **Corolla** 6-12 mm diam., ± rotate to shallowly campanulate; inside with dark purple-brown to purple-black or purple-red spots on cream to yellow background, often with dark colour coalescing towards apex of lobes into solid patch, sometimes forming narrow ring around corona; **lobes** 2.6-4.0 mm long, 1.7-2.0 mm broad at base, ascending to spreading, deltate, not thickened towards apex, with cilia up to 1 mm long along margins. **Corona** 2.1-2.3 mm diam., purple-red to purple-black, raised on short stipe; **outer lobes** erect, bifid to above middle into slightly diverging lobules; **inner lobes** ± equalling anthers, deltoid to ± square, obtuse to truncate, dorsiventrally flattened, with short ascending to erect truncate emarginate ridge-like dorsal projection near base.

Distribution and habitat

Subsp. *confusa* is fairly widely distributed in the Knersvlakte of southern Namaqualand from Hol River west of Vredendal to the foot of the Langeberg and to Loeriesfontein. It is restricted to firm, reddish loamy sands, mainly along the Sout River, where it generally grows in flattish areas to gentle lower slopes, often among small bushes of the gregarious *Ruschia comptonii*, *R. subsphaerica* or *R. spinosa*.

Diagnostic features and relationships

In subsp. *confusa* the pedicel is relatively short but has a descending apex so that the flowers are nodding. The corolla is mostly fairly small and is very variably coloured, though it is never as prettily coloured as in some of the other subspecies. The lobes may be nearly wholly dark purple-brown or they may be spotted with purple-red on a cream to yellow background. Towards the centre the cream or yellow colour predominates and sometimes it also has a fine darker spotting.

The dark corona is short and there is hardly any basal stipe. It consists of short outer lobes, which are only shallowly bifid towards their apices, and very short inner lobes, which spreading, faintly toothed dorsal projection almost as long as the lobes themselves.

History

Subsp. *confusa* was first collected by H. Hall (see under *Huernia hallii*) in November 1957 north of the Sout River and it was described by Plowes as *Quaqua confusa* from material that he collected in September 1969 near the foot of Vanrhyn's Pass.



Fig. 13.41. *Q. parviflora* subsp. *confusa*, PVB 5999, foot of Vanrhyn's Pass.



Fig. 13.42. *Q. parviflora* subsp. *confusa*, PVB 6068, south-west of Loeriesfontein.

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5. *Quaqua bayeriana*

Quaqua bayeriana (Bruyns) Plowes, *Excelsa* 16: 93 (1994).

Quaqua parviflora subsp. *bayeriana* Bruyns, *Bradleya* 1:52 (1983).

Type: Cape, about 20 miles south-west of Springbok, Bruyns 1464 (NBG).

Stems 10-20 mm thick. **Pedice** 2-4 mm long, descending and holding flower facing downwards. **Corolla** 6-8 mm diam., $\pm$ rotate to shallowly campanulate; inside with thin pale purple twisted hairs, pale yellow-green to cream with irregular pale red to purple-red or pale brown spots and larger patches; **tube** shallow, containing base of column, with corolla slightly thickened near mouth; **lobes** 2.5-3.0 mm long, 2 mm broad at base, ascending to spreading, deltate. **Corona** 2.2-2.5 mm diam., purple-brown to black, raised on short stipe; **outer lobes** $\pm$ 0.6 mm long, erect, bifid to above middle into $\pm$ deltate slightly diverging lobules; **inner lobes** 0.3-0.5 mm long, shorter than to $\pm$ equalling anthers, deltoid to $\pm$ square, obtuse to truncate, dorsiventrally flattened, with short erect truncate emarginate ridge-like dorsal projection near base.

Distribution and habitat

Quaqua bayeriana is known from the Messelpad, south-west of Springbok, where it is locally quite common. It has also been recorded from Komaggas.

It grows on south- or west-facing slopes of gneiss or quartzite hills of the Nama series among quite dense vegetation, mainly consisting of *Eriocephalus* shrubs and a few succulents.

Diagnostic features and relationships

Plants of *Q. bayeriana* have stems that are difficult to separate from those of *Q. incarnata* subsp. *hottentotorum* except for the lack of the broader peduncular patches which are typical of the latter. Here they are replaced by very small patches on which the flowers are very sparse.

Flowers of *Q. bayeriana* are held on fairly short, usually decurved pedicels so are nodding. The corolla is small, with short, deltate lobes. They have turned out to be very variable in the colouring of the inside: flowers on the original plant collected had pale brown markings on cream but more recent collections have been marked with pale red to red-purple on pale yellow. The inside of the corolla has many fine hairs on it, in addition to the fine cilia along the margins of the lobes.

The corona is small as well and is seated on an indistinct stipe. It has very short outer lobes, which are only slightly bifid at the apex. The inner lobes are also short and have a ridge-like dorsal projection near the base which is in series with the outer lobes.

The shape and size of the flowers and the

colouring in some of them is very suggestive indeed of *Q. parviflora* subsp. *confusa* and the two also have similar coronas. They differ mainly in the presence of hairs on the corolla in *Q. bayeriana*. Although *Q. bayeriana* is surrounded by a variety of forms of *Q. parviflora*, all of these are referable to subsp. *parviflora* and there is no evidence of intergradation between *Q. bayeriana* and any of these.

History

Quaqua bayeriana was first collected near Komaggas by a Mr. Pienaar. It was named in honour of M. Bruce Bayer.

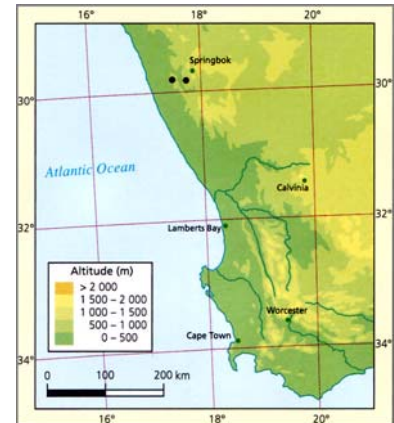


Fig. 13.43. Distribution of *Quaqua bayeriana*.



Fig. 13.44. *Q. bayeriana*, PVB 1464, Wildeperdehoek Pass.



Fig. 13.45. *Q. bayeriana*, PVB 1464, Wildeperdehoek Pass.

6. *Quaqua pallens*

Quaqua pallens Bruyns, Bot. Jahrb. Syst. 121: 355

(1999). Type: South Africa, Cape, near Garies, Bruyns 6767 (BOL).

Stems 60-300 mm long, 6-12 mm thick, erect though often scandent in bushlets, grey-green to purple-black mottled with grey. **Pedicel** (2-) 3-5 mm long, ascending and holding flower facing partly upwards. **Corolla** 4-8 mm diam., rotate; outside pale green; inside glabrous, lobes pale green towards tips sometimes becoming suffused with pale red towards base, rest of corolla white; **tube** shallow around base of gynostegium; **lobes** ± 3 mm long, 1.5 mm broad at base, spreading to reflexed, linear-lanceolate, acute, margins not folded back, without cilia. **Corona** ± 2 mm tall, 2.5 mm broad, yellow-green to white, narrowing towards base and without stipe; **outer lobes** ± 1 mm long, ascending, bifid into widely diverging lobules; **inner lobes** ± 0.5 mm long, exceeding anthers and meeting in centre, rectangular, truncate, dorsiventrally flattened, dorsally swollen near base but otherwise without dorsal projection.



Fig. 13.46. *Q. pallens*, PVB 7584, near Garies.

Distribution and habitat

Quaqua pallens is found in the hills north of Garies where it is locally quite plentiful. Plants grow on gneissic slopes inside bushes and at one locality were quite often encountered inside small clumps of *Crassula brevifolia*.

Diagnostic features and relationships

Specimens of *Q. pallens* are often scandent in bushes and the stems are then up to 300 mm long and slightly stouter. Some more exposed specimens that were found were more slender than usual and had a darker colour. The younger stems are often noticeably mottled.

Flowers are borne in small numbers, often on quite large peduncular patches. They are held facing partly upwards on fairly long pedicels. On the inside the flowers are pale green towards the tips of the lobes and become white towards the centre without any darker spots or bars. They are fairly small, with spreading to reflexed and relatively narrow

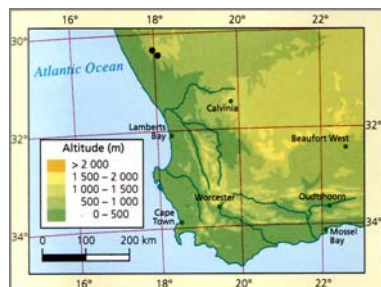


Fig. 13.47. Distribution of *Quaqua pallens*.

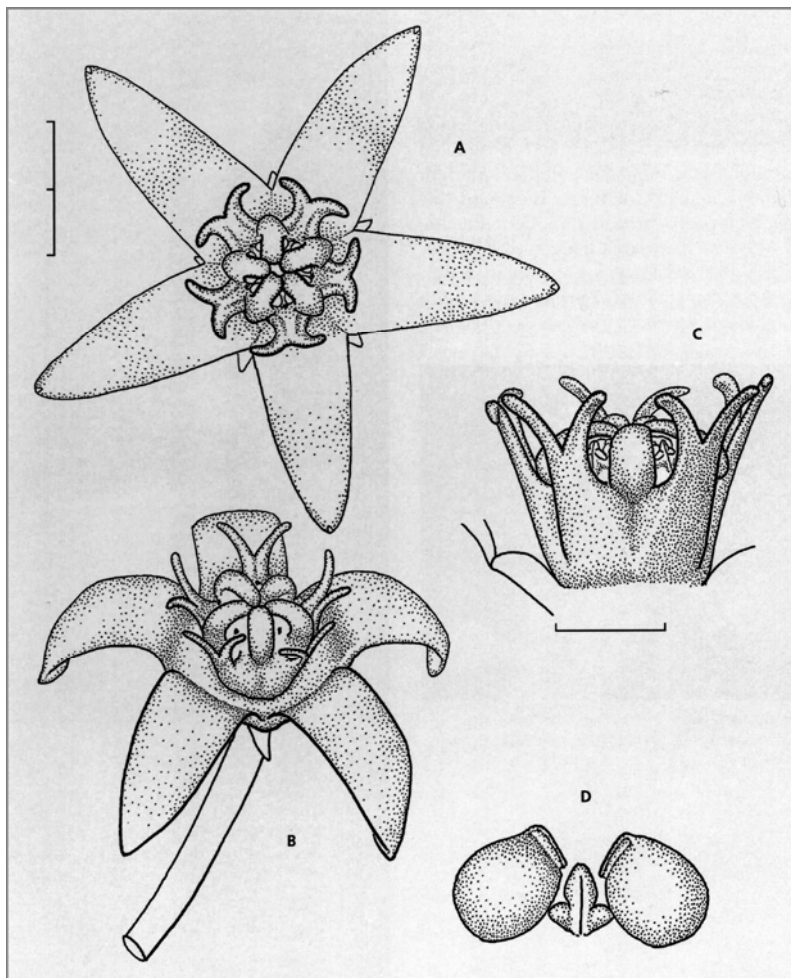


Fig. 13.48. *Quaqua pallens*. A, face view of $\pm$ flat flower. B, oblique view of flower with petals partly reflexed. C, side view of gynostegium. D, pollinarium. Scale bars: A, B, 2 mm (at A); C, 1 mm (at C); D, 0.25 mm (at C). Drawn from: PVB 6767, near Garies.

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lobes. There are no hairs on the corolla, either inside or along the margins of the lobes.

The corona is altogether nearly white and lacks any clear basal stipe. It has slender, ascending, deeply bifid outer lobes. The inner lobes are entirely without dorsal projections but mostly cover the anthers completely.

The colouring, orientation and shape of the corolla as well as the pale corona with its long, deeply bifid outer lobes all suggest that the closest affinities of *Q. pallens* lie with *Q. parviflora* subsp. *parviflora*, in which the flowers can also be relatively small. Although the barring of purple on the flower can become quite faint in subsp. *parviflora*, it has never been observed to be absent and the flowers of *Q. parviflora* always have fine cilia along the margins of the lobes. The mottling observed on some of the stems is not known in any of the closely related species.

History

Quaqua pallens was first observed by Jacobus Pieter 'Jan' van Zanten (11 March 1931 - 30 June 1994). Van Zanten was a clerk at ISCOR in Pretoria but devoted much of his spare time to collecting stapeliads and he explored particularly in Namaqualand and southern Namibia looking for them. He found this species probably around 1975, but no details of where he discovered it are available. Only in July 1996 did I manage to relocate it near Garies and another locality was discovered in July 1998, not far from the first.



Fig. 13.49. *Q. pallens*, PVB 7584, near Garies. The mottled stems characteristic of this species are clearly visible here.

7. Quaqua pulchra

Quaqua pulchra (Bruyns) Plowes, *Excelsa* 16: 93 (1994).

Quaqua parviflora subsp. *pulchra* Bruyns, *Bradleya* 1: 52 (1983).

Type: South Africa, Cape, Hol River Station, Bruyns 1397 (NBG).

Small succulent forming clump 60-300 mm diam. **Stems** 15-25 mm thick, erect to decumbent, grey-green; **tubercles** 4-10 mm long, conical, spreading to slightly decurved, each tipped with sharp hardened yellow tooth. **Inflorescences** of 1-3 usually successively opening flowers

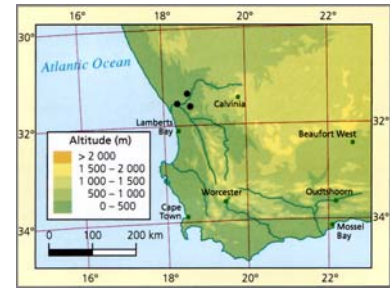


Fig. 13.50. Distribution of *Quaqua pulchra*.



Fig. 13.51. *Q. pulchra*, PVB 1397, west of Hol River Siding, Vredendal.

towards tips of stems; **pedicel** 2-4 mm long, initially horizontal or ascending then descending, holding flower facing downwards. **Corolla** 8-16 mm diam., $\pm$ rotate; **outside** pale green suffused with red; inside in upper half to two thirds of lobes bright to pale yellow or yellow-green, below this cream dotted and lined with pale purple-red to maroon, this darker colour organised into 1-3 concentric rings around and below mouth of tube, becoming darker towards base of tube; **tube** shallow, containing only base of gynostegium; **lobes** 4.0-8.0 mm long, 1.5-2.5 mm broad at base, spreading, upper yellowish portion somewhat thickened, narrowing very gradually from base to abruptly acute tip, with slender (not spatulate) cilia up to 2 mm long along margins, with thin pale purple twisted hairs on inside below thickened portion (on maroon/purple-red area). **Corona** 2.5-3.0 mm diam., pale purplish red, raised on stipe up to 0.5 mm long; **outer lobes** 1.0-1.3 mm long, ascending, deeply bifid into widely divergent lobules, fused laterally to inner lobes at base only; **inner lobes** $\pm$ 0.5 mm long, sometimes exceeding anthers, deltoid to rectangular, obtuse to truncate-emarginate, dorsiventrally flattened, dorsally swollen near base but otherwise without dorsal projection.

Distribution and habitat

A narrow endemic from the Knersvlakte of southern Namaqualand, *Q. pulchra* is found from north of Vanrhynsdorp to just west of Lutzville.

Although the Knersvlakte is most famous for its patches of quartz gravel with their unusual flora, this species is not found on these habitats but rather in the firm, red sands and loams along the Sout and lower Olifants rivers. Here it is usually associated with small shrublets of the gregarious species *Ruschia comptonii* and *R. subsphaerica* and with *Euphorbia muricata* and other small succulents.

Diagnostic features and relationships

Plants mostly have fairly thick stems with stout and often decurved tubercles arranged into four neat angles. In this respect they bear some resemblance to plants of *Q. inversa*.

The flowers develop from tiny peduncular patches which sometimes etiolate to a small peduncle up to 3 mm long (as in *Q. parviflora* and *Q. inversa*) and they are held facing downwards on a short pedicel.

Quaqua pulchra has remarkably beautiful flowers. They are more or less flat, with a very shallow tubelet around the gynostegium and with spreading lobes whose apices are somewhat thickened. On the inside the lobes are yellow or yellowish green, which merges gradually into a mottling of red to maroon around the base. The mouth of the tube is usually mottled or barred with this darker colour on a white background, with the white background usually forming at least one ring but sometimes as many as three. The patches of red to maroon may be rather pallid, however, and one plain yellow-flowered plant was also once found near Vredendal (Bruyns 1983). Flattened and much crinkled hairs are found on the inside of the flower on the darker, lower part of the corolla lobes only. There are also plenty of long, very slender cilia along the margins of the lobes. These are somewhat longer than the hairs on the corolla and are fine (not clavate at all) and rather untidily spreading and intertwined.

The corona is reddish. It consists of slender outer lobes which are bifid into strongly spreading, almost filiform lobules towards their apices and are lightly channelled towards their bases. The inner lobes are small and are without any trace of a dorsal projection.



Fig. 13.52. *Q. pulchra*, Nagel, west of Lutzville.



Fig. 13.53. *Q. pulchra*, Nagel, west of Lutzville.

History

Quaqua pulchra was discovered by H. Hall (see under *Huernia hallii*) to the west of Vredendal on the banks of the Olifants River on the farm Liebendal in March 1969. The natural vegetation in this area has, unfortunately, now almost all been destroyed by viticulture but the species occurs at other spots in the vicinity.

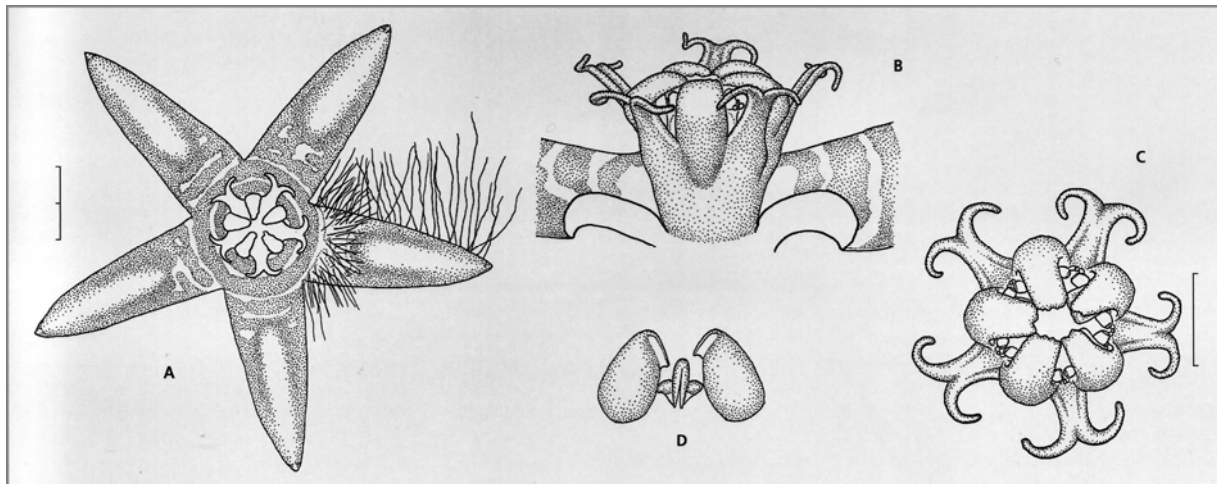


Fig. 13.54. *Quaqua pulchra*. A, face view of flower. B, side view of gynostegium and centre of dissected flower. C, face view of gynostegium. D, pollinarium. Scale bars: A, 2 mm; B, C, 1 mm (at C); D, 0.25 mm (at A). Drawn from PVB 1397, west of Hol River Siding, Vredendal.

QUAQUA INVERSA

8. *Quaqua inversa*

Quaqua inversa (N.E.Br.) Bruyns, *Bradleya* 1: 53 (1983).

Caralluma inversa N.E.Br., *Gard. Chron.* Ser. 3, 33: 354 (1903).

Type: South Africa, Cape, Clanwilliam district, Ayres sub *N.S. Pillans* 92 (K, holo.; BOL, iso.).

Caralluma villetii C.A.Luckh., *S. African Gard. & Country Life* 25: 96 (1935).

Type: Cape, Vanrhynsdorp district, *Villet sub Lückhoff* 226 (BOL).

Small succulent forming clump 60-300 mm diam. **Stems** 50-250 mm long, 10-25 mm thick, erect, greyish to purplish green; **tubercles** 4-10 mm long, stoutly conical, spreading to slightly decurved, joined at bases into 4 angles along stem, each tipped with sharp hardened yellow tooth. **Inflorescences** of 1-3 usually successively opening flowers towards tips of stems; **pedicel** 2-8 mm long, < 1 mm thick, spreading with flower facing horizontally to descending and holding flower facing downwards (rarely upwards); **sepals** 1.5-2.5 mm long, lanceolate, acute. **Corolla** 10.5-15.0 (-21) mm diam., $\pm$ rotate; outside pale reddish green; inside with lobes pale yellow or green in upper half to third and pale to wine-red to maroon (sometimes spotted and barred with white) below and onto united part becoming faintly red-spotted on white background in tube, glabrous and smooth; **tube** 1.0-2.5 mm deep, broadly conical to shallowly bowl-shaped, corolla slightly thickened around mouth; **lobes** 3.5-8.0 mm long, 2-3 (-4) mm broad at base, ascending to spreading, ovate-lanceolate, acute,

upper yellow to green portion slightly thickened, margins slightly recurved and with spatulate purple cilia up to 2 mm long. **Corona** 1.5-3.5 mm diam., dark maroon to red (occasionally pink), raised on short stipe < 0.5 mm long; **outer lobes** 1.0-1.5 mm long, ascending, linear, often notched or slightly bifid at apex, lightly channelled down inner face towards base, fused laterally to inner lobes at base only; **inner lobes** $\pm$ 0.5 mm long, adpressed to backs of and usually covering anthers entirely, linear, truncate-emarginate, dorsiventrally flattened, usually with conspicuous spreading to erect truncate-emarginate ridge-like dorsal projection.

Distribution and habitat

Quaqua inversa is a rare species which is endemic to the central parts of Namaqualand. It is known from a few widely scattered localities west of the escarpment from Nuwerus, Bitterfontein and Kotzesrus in the south to near Port Nolloth in the north. I have not been able to locate it any further south than Nuwerus and remain doubtful of Bolus' locality of 'Vanrhynsdorp' and the original locality of Ayres from the 'Clanwilliam district'.

It is found usually on firm, red sand or gneissic ground on low, rolling hills among small shrublets belonging to the succulent Aizoaceae. Several of the spots where it has been seen are sparsely covered with trailing species of *Cephalophyllum*.

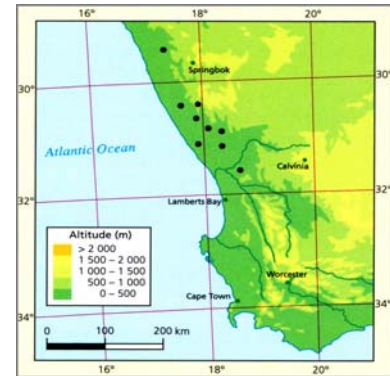


Fig. 13.55. Distribution of *Quaqua inversa*.

Diagnostic features and relationships

Plants of *Q. inversa* may be quite substantial and can reach 300 mm in diameter. The stems are adorned with stoutly conical, often somewhat decurved tubercles which are joined into four neat angles. The tubercles are often a little stouter and have a more conspicuous, yellow tip than those in *Q. incarnata* or *Q. parviflora*,

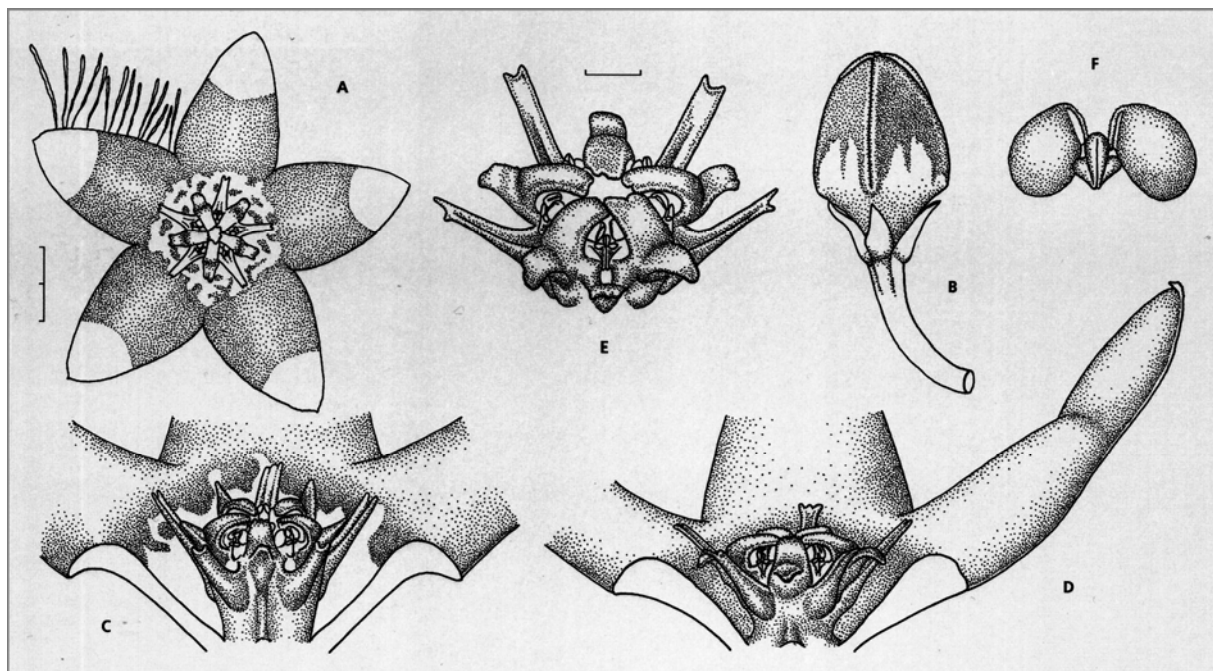


Fig. 13.56. *Quaqua inversa*. A, face view of flower. B, bud. C, D, side view of dissected flower. E, face view of gynostegium. F, pollinarium. Scale bars: A, B, 2 mm (at A); C, D, 1 mm (at A); E, 0.5 mm; F, 0.25 mm (at A). Drawn from: A, B, C, E, F, *PVB* 4578, north-east of Bitterfontein; D, *PVB* 6133, west of Bitterfontein.



Fig. 13.57. *Q. inversa*, PVB 6336, near Wallekraal, with nearly completely flat flowers.

with which it frequently grows.

Flowers of *Q. inversa* are probably the most beautiful in the genus. The original specimen of '*Caralluma villetii*' had flowers 21 mm in diameter according to Lückhoff but mostly they are quite a lot smaller than this, although they are noticeably larger than in *Q. parviflora*. In most specimens the flower modestly hides its beauty by facing downwards and it has to be lifted up to be admired. However, a few specimens have been seen where the flower faces horizontally or even a little upwards. It usually opens to be more or less flat with a small, conical tube in the centre but again among recent collections plants have been seen where the tube is absent. On the inside, the upper part of each corolla lobe is generally pale yellow. The remainder of the lobe and the mouth of the tube is a deep wine-red to maroon (although a few with pale red have also been seen), mostly uniformly coloured but sometimes particularly attractively mottled with white. The tube or the centre of the flower (when the tube is absent) is white, often faintly and finely mottled with red. It has been found that the flowers emit a faint, fruity odour for a while after opening.

When it is present, the tube contains the whole of the corona. In *Q. inversa* the corona is variable in colour, from dark maroon to red or even pinkish and this is usually dependent on the darkness of the rest of the corolla. The outer lobes are more or less parallel with the sides of the tube. They may be linear, with an obtuse apex, or they may be slightly bifid at the apex with spreading lobules. The inner lobes mostly cover the anthers and they have an ascending to spreading, tooth-like dorsal projection.



Fig. 13.58. *Q. inversa*, PVB 6133, west of Bitterfontein.



Fig. 13.59. *Q. inversa*, PVB 6133, west of Bitterfontein.



Fig. 13.60. *Q. inversa*, PVB 6133, west of Bitterfontein.

This dorsal projection is another very variable feature of the flower. It may be anything from conspicuous to nearly absent. In cases where it is conspicuous, it may almost equal the outer lobes so that the whole structure appears to have 10 outer lobes.

This species is very similar to *Q. cincta* and, if one ignores the distinctive colouring that each has, there is little to separate them. Formerly I claimed (Bruyns 1983) that the two were separated by the orientation of the pedicel as well as other features but this character has subsequently proved to be variable in both. Thus the two are separated chiefly by their very different colouring and the more deeply channelled and deeply bifid outer corona lobes of *Q. cincta*. Vegetatively, they can be distinguished by the much more stoutly toothed stems of *Q. inversa*.

History

Quaqua inversa was first collected by Charles Ayres in 1902, ostensibly in the 'Clanwilliam district' but, as mentioned above, it is not known today from anywhere so far south. Ayres was a nurseryman from England (born in Bristol in winter 1848) who started a nursery in Wandel Street in Cape Town in 1876 and a florist shop a year later in St George's Street. He was interested in indigenous plants and collected in the Free State and the northern part of the Cape. He died in a pony-trap accident on 24 January 1915. The material on which Carl Lückhoff based the name *Caralluma villetii* was collected by Charles T and Elizabeth M. Villet in 1934 somewhere near Vanrhynsdorp.

QUAQUA CINCTA

9. *Quaqua cincta*

Quaqua cincta (C.A.Lückh.) Bruyns, *Asklepios* 65: 17 (1995).

Caralluma cincta C.A.Lückh., *S. African Gard. & Country Life* 25: 57 (1935).

Quaqua inversa var. *cincta* (C.A.Lückh.) Bruyns, *Bradleya* 1: 56 (1983).

Type: South Africa, Cape, Sout River Bridge, *Primos* sub Lückhoff 161 (BOL).

Small succulent forming clump 60-300 mm diam. **Stems** 50-250 mm long, 15-20 mm thick, erect, purplish green; **tubercles** 3-6 mm long, conical, spreading, joined towards bases into 4 angles along stem, each tipped with sharp hardened yellowish tooth. **Inflorescences** of 1-2 usually successively opening flowers towards tips of stems; **pedicel** 4-12 mm long, <1 mm thick, usually ascending and holding flower facing upwards; **sepals** 2-3 mm long, ovate-lanceolate, acute. **Corolla** 14.5-21.0 mm diam., rotate; outside purple in upper half of lobes changing to cream to pale green below, with raised purple stripe down middle of lobe; inside dark purple to purple-brown on lobes (occasionally purple-brown spotted on cream towards base of lobes), below lobes and on sides of tube with 3 concentric rings of purple-brown on cream, base of tube cream, glabrous and smooth; **tube** 1.2-2.0 mm deep, broadly conical, containing column, with corolla slightly thickened at mouth; **lobes** 5.5-8.0 mm long, 3-5 mm broad at base, spreading, margins slightly folded back, with spatulate cilia up to 2 mm long except near tips and base. **Corona** 3.3-4.5 mm diam., dark purple becoming yellow towards base (sometimes yellow only with purple margins), raised on very short stipe (< 0.25 mm long); **outer lobes** 0.7-1.5 mm long, ascending-spreading, deeply bifid into diverging and somewhat

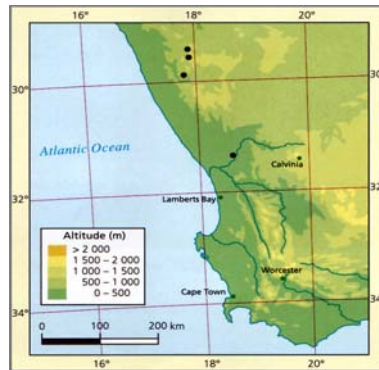


Fig. 13.61. Distribution of *Quaqua cincta*.

dorsiventrally flattened lobules, deeply channelled down whole of inner face, fused with inner lobes at base only; **inner lobes** ± 0.5 mm long, adpressed to backs of anthers and usually shorter than or equalling them, $\pm$ deltoid to $\pm$ rectangular, truncate-emarginate, dorsiventrally flattened, with conspicuous erect to spreading truncate-emarginate dorsal projection.

Distribution and habitat

Today *Q. cincta* is known from the type collection which was supposed to have originated from the Sout River and from several records in the hills around Springbok. Here it is found in the Nama quartzites south-west of Spring-



Fig. 13.62. Richard Primos (front) with friends on Table Mountain in the 1950s (courtesy N. Moralee).

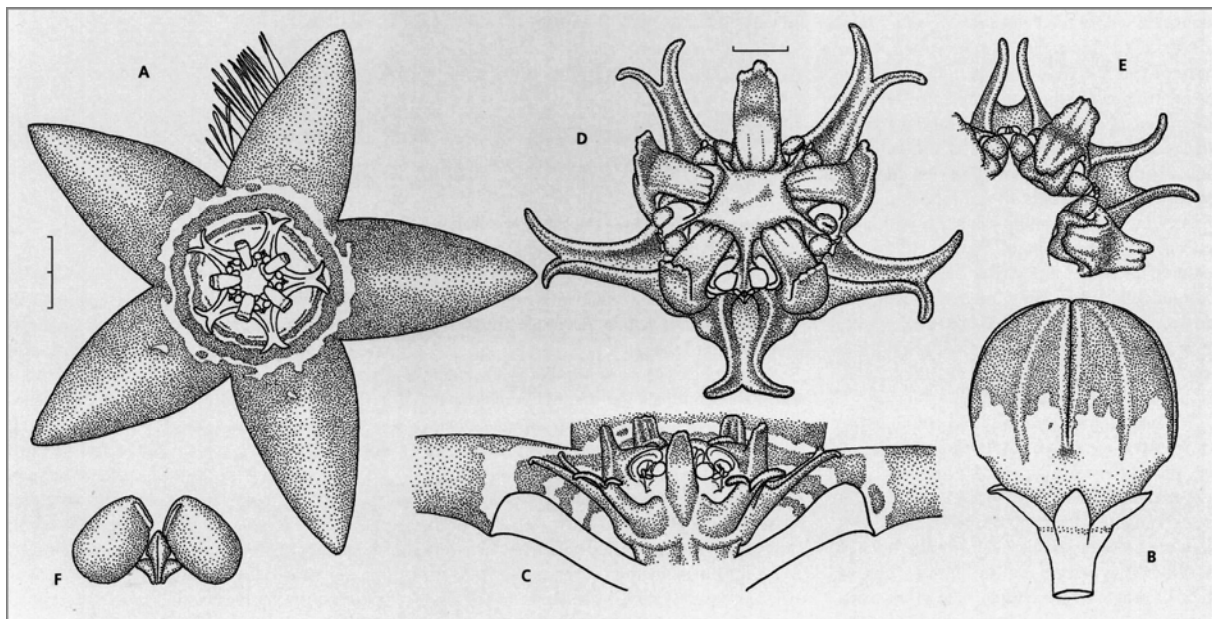


Fig. 13.63. *Quaqua cincta*. A, face view of flower. B, bud. C, side view of dissected flower. D, E, face view of gynostegium. F, pollinarium. Scale bars: A, B, 2 mm (at A); C, 1 mm (at A); D, E, 0.5 mm (at D); F, 0.25 mm (at A). Drawn from PVB 5161, north of Concordia.

bok and also in gneiss to the north-east around Okiep and Concordia.

Plants usually grow on stony slopes under bushes or in clumps of *Ruschia robusta* in gravelly flats but I have even seen it on an exposed gneiss whaleback growing in a clump of *Polymita albiflora*. It is generally not common and plants have to be diligently searched for.

Diagnostic features and relationships

Specimens of *Q. cincta* may form clumps up to 300 mm in diameter. The stems are not in any way noteworthy and could easily belong to one of several other species that grow in the same area, such as *Q. acutiloba*, *Q. incarnata* or *Q. parviflora*.

In *Q. cincta* the pedicels are of very variable length and were recorded at 5 mm long in Primos' plant but are up to 12 mm long in some of my own collections. They usually, but not always, hold the flower facing upwards. The flower in *Q. cincta* is of quite a significant size for a species in this section. It is usually at least 15 mm in diameter and was 21 mm wide in the plant that Lückhoff saw. The flowers emit a foul, excrement-like odour.

In this species the corolla is very boldly coloured inside with a patterning which is in fact very similar to that of *Q. parviflora* subsp. *swanepoelii*, just on a larger scale. The lobes, whose edges are adorned with tufts of quite shaggy, spatulate cilia, are dark purple to red-brown. In Primos' plant this colour was suddenly interrupted by a ring of cream at the base of the lobes. However, it has often been observed that the dark colour of the lobes begins to break up before their bases with an irregular mottling of cream, as was found also Meve (1987). At the bases of the lobes and on the sides of the tube there are three concentric rings of the same dark colour of the lobes on a cream background. These rings become thinner as one descends in the tube, the lowest one being very fine and often somewhat broken up.

Despite the fact that it is raised above the base on a stipe, the entire corona fits neatly into the tube. The dainty outer lobes are ascending, deeply channelled on the inner surface and



Fig. 13.65. *Q. cincta*, PVB 7284, Okiep.



Fig. 13.64. *Q. cincta*, PVB 5161, north of Concordia.

bifid at their tips. They and the inner lobes are at least partly dark purple (often just along the margins), becoming yellow towards their bases. The inner lobes are more or less rectangular and have a usually erect and mostly quite conspicuous dorsal ridge near their base.

History

Richard Primos discovered *Q. cincta* in 1932 and there has been some confusion in the literature over where he found it. C.A. Lückhoff gave the type locality as Touws River when he published the species, but it was changed in White & Sloane (1937) to Sout River, which lies north of Vanrhynsdorp and one must assume

that this was on the advice of Lückhoff himself. However, the species has never been seen again quite so far south.

Primos (28 January 1888-27 March 1969), of Greek extraction, lived all his life in Cape Town, where he had his own small but quite successful importing business. He had a keen interest in succulent plants (though he never collected them on any scale) and was also an enthusiastic and long-term member of the Mountain Club of South Africa. *Titanopsis primosii* was named after him.

For many years after *Q. cincta* was discovered it remained obscure and the next recorded collection was made south-west of Springbok by Walter Wisura in 1972.



Fig. 13.66. *Q. cincta*, PVB 5161, north of Concordia, plant with unusually rotund buds (one visible in background).

III. *Quaqua* sect. *Quaqua*

Key to the species

1. Tubercles on stems obtuse and rounded with teeth (if present) less than 2 mm long 2.
2. Corolla smooth inside 18. *Q. linearis*
2. Corolla papillate inside 19. *Q. ramosa*
1. Tubercles tapering into a conical tooth, teeth longer than 3 mm 3.
3. Inside of corolla wholly yellow, cream or white, always with small papillae at least in mouth of tube 4.
4. Corolla with small adpressed bristles all over inside, tube not quite containing corona 10. *Q. aurea*
4. Corolla inside with small adpressed bristles restricted to mouth of tube and bases of lobes, tube containing corona 5.
5. Corolla lobes uniformly wide for most of length, pentagonal shape of gynostegium given by broad area below outer corona lobes 12. *Q. framesii*
5. Corolla lobes narrowing from or near base, pentagonal shape of gynostegium given by limb of outer corona lobes or by inner lobes 11. *Q. incarnata*
3. Corolla lobes dark purple-black to maroon (if yellow then without small papillae in mouth of tube) 6.
6. Corolla lobes oblong-ovate, inside spotted and mottled with purple-brown or maroon on cream 17. *Q. pillansii*
6. Corolla lobes not as above, inside uniformly dark purple-black or red 7.
7. Tubercles on stem arranged clearly into 4 vertical wings 15. *Q. arenicola*
7. Tubercles on stems rather irregularly arranged into 4-5 angles but not joined clearly into vertical wings 8.
8. Corolla lobes $\pm$ uniformly broad for most of length, narrowing abruptly to strongly incurved tips, papillae in mouth of tube conical, often aggregated into partially fused clusters 14. *Q. multiflora*
8. Corolla lobes tapering from near base to acute apex, not or only slightly incurved at tips, papillae in mouth of tube mostly low and rounded 9.
9. Plant rooting by central stem only and forming $\pm$ erect shrub, mouth of tube and base of lobes roughly bristly-papillate inside 16. *Q. mammillaris*
9. Plant spreading and mat-forming, rooting on side-branches, mouth of tube finely bristly-papillate (scarcely visible to naked eye) or glabrous inside 13. *Q. armata*

The last four species are rather difficult to separate reliably in a key: vegetatively *Q. arenicola* can usually be distinguished from the others by the neat arrangement of the tubercles into four rows; plants of *Q. multiflora* can be very roughly spiny (and, in the field, often tend to root by a single central stem only) as in *Q. mammillaris* and plants of *Q. mammillaris* can sometimes spread out in a nearly mat-forming manner. Florally, though, *Q. multiflora* cannot easily be confused with the last two. *Q. mammillaris* and *Q. armata* are usually easily distinguished when in flower by the longer, more slender and gradually tapering lobes in *Q. mammillaris* with a very rough indumentum of papillae towards their bases. In *Q. armata* the corolla lobes are broader and narrow more rapidly to their tips.

The five taxa 'aurea', 'framesii', 'hot-tentatorium', 'incarnata' and 'tentacuiata' are recognised at different levels. In all of these the stems are quite similar, with stout conical teeth (slightly flattened above) subtended sporadically by stipular denticles and many fairly broad peduncular patches in the upper parts. The flowers are always yellow, cream or white inside and usually pinkish outside. On the inside, at least in the mouth of the corolla tube and on the base of the lobes, there are many short, thick bristles which sometimes arise from a low, rounded papilla. These bristles vary somewhat in length: they are longest in 'incarnata' and 'framesii' and shortest in 'hot-tentatorium' and 'tentacuiata'.

10. *Quaqua aurea*

Quaqua aurea (C.A.Lückh.) Plowes, *Excelsa* 16: 90 (1994).

Caralluma aurea C.A.Lückh., 'S. A. G.' 29: 94 (1938).
Quaqua incarnata subsp. *aurea* (C.A.Lückh.) Bruyns, *Bradleya* 1:43 (1983).

Type: South Africa, Cape, top of Botterkloof Pass, Villet sub Lückhoff 269 (BOL).

Small succulent forming clump 60-300 mm diam. **Stems** 50-150 mm long, 15-25 mm thick, decumbent, grey-green; **tubercles** 3-6 mm long, conical, spreading, joined near base into 4-5 angles along stem, each tipped with sharp yellow tooth, usually with 2 denticles near base. **Inflorescences** of 3-10 $\pm$ simultaneously opening flowers towards apex of stem; **pedicel** 1-2 mm long, 1 mm thick, holding flower facing horizontally; **sepals** $\pm$ 1.5 mm long, 1 mm broad at base, lanceolate. **Corolla** 15-22 mm diam., campanulate to nearly rotate; outside pinkish becoming paler towards base; inside white in centre becoming cream to pale yellow towards tips and slightly greenish towards edges, covered with minute ascending bristles except towards margins and apices of lobes; **tube** $\pm$ 1.0 mm deep, broadly V-shaped, nearly containing column; **lobes** 5-9 mm long, 2-3 mm broad at base, always somewhat ascending, margins only slightly folded back with folding starting somewhat above base, obtuse tip slightly incurved. **Corona** 1.3-1.7 mm tall, 2.5-2.9 mm broad, bright yellow, gradually narrowing to base and without stipe; **outer lobes** $\pm$ 0.8 mm long, erect, bifid into erect slightly diverging deltoid acute teeth, fused laterally in lower half to bases of inner lobes and so forming pouch enclosing guide-rails; **inner lobes** $<$ 1 mm long, adpressed to backs of anthers and slightly exceeding them, linear, obtuse to truncate, dorsiventrally flattened, dorsally swollen near base but otherwise without dorsal projection.

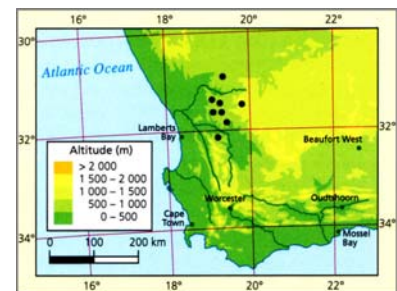


Fig. 13.67. Distribution of *Quaqua aurea*.

Distribution and habitat

Quaqua aurea is found on the plateau (at 700-800 m) above the escarpment east of Vanrhynsdorp from Nieuwoudtville eastwards towards Calvinia. To the south it also occurs to the area around the Doring River near Botterkloof and in the Biedouw Valley. It has also recently been collected near the foot of Kubiskow Mountain north of Loeriesfontein (PVB 7942) at an altitude of about 900 m. In the Biedouw Valley and around Botterkloof it grows at significantly lower altitudes (300-350 m).

In the Biedouw Valley and around Botterkloof it may be fairly common among small, scattered bushes at the base of stony slopes.

Above the escarpment plants occur mainly in flat areas that are quite densely covered by small shrubs of *Ruschia spinosa*, *Pteronia glomerata* or *Eriocephalus*, as are typical of the so-called 'Western Mountain Karoo' which occurs in these areas. Here they are often found growing socially with *Pectinaria maughanii* and sometimes with *Orbea ciliata* and *Piранthus punctatus*.

Diagnostic features and relationships

Plants of *Q. aurea* are indistinguishable from those of the various southern forms of *Q. incarnata* and form clumps up to 300 mm in diameter with relatively stout stems, where many of the

tubercles bear small, stipular denticles.

As in most species in this section, the flowers are produced in large numbers towards the tips of the stems on 'peduncular patches' and they are borne on very short pedicels. The flowers themselves are rather pretty. Inside they are cream towards the tips of the lobes with this colour becoming fainter and tending to white in the centre. The fairly narrow lobes spread out (but not fully against the stem) and there is a shallow, broadly V-shaped corolla tube from which the tips of the outer corona lobes usually project. The inner surface is covered with short bristles, though this is only clearly visible under a microscope. The flowers emit a sharp and sourish honey-like scent.

The comparatively large corona, which is

almost entirely contained in the corolla tube, is bright yellow. It consists of outer lobes which are almost erect and divided into deltoid lobules, and inner lobes which cover the anthers and are slightly dorsally swollen.

History

Quaqua aurea was described from material collected by Charles T. Villet which flowered in October 1938. It seems to have been recorded for the first time by R.H. Compton in 1926. This material was known to N.S. Pillans but, according to the records in the Bolus Herbarium, he seems to have been unsure whether to describe it as a distinct species or as a variety of what was then *Caralluma incarnata*.



Fig. 13.68. *Q. aurea*, PVB 5994, Biedouw Valley.



Fig. 13.69. *Q. aurea*, PVB 7982, north-east of Nieuwoudtville.

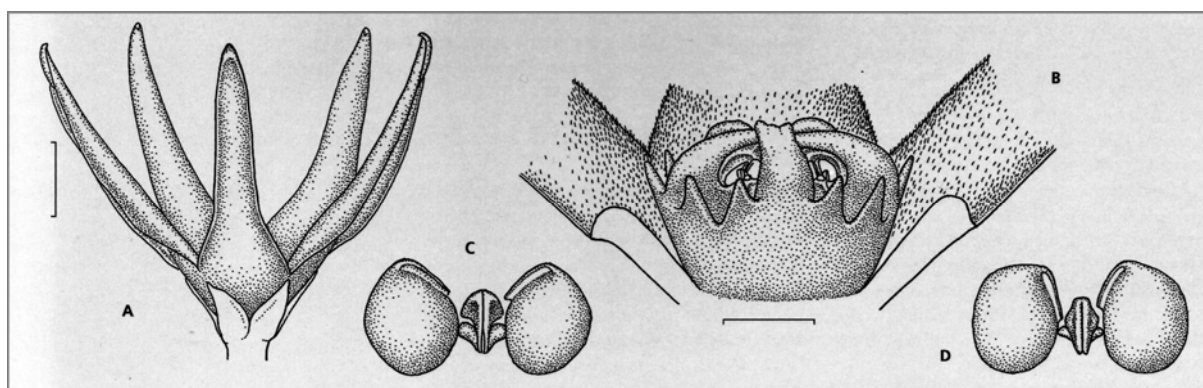


Fig. 13.70. *Quaqua aurea*. A, side view of flower. B, side view of centre of dissected flower. C, D, pollinarium. Scale bars: A, 2 mm; B, 1 mm; C, D, 0.25 mm (at A). Drawn from: D, PVB 1107, east of Nieuwoudtville; rest, PVB 5994, Biedouw Valley.

QUAQUA INCARNATA

11. *Quaqua incarnata*

Quaqua incarnata (L.f.) Bruyns, *Bradleya* 1: 39 (1983).

Stapelia incarnata L.f., Suppl.: 171 (1781).

Podanthes incarnata (L.f.) Sweet, *Hort. Brit.*, ed. 2: 358 (1830).

Piранthus incarnatus (L.f.) G.Don, *Gen. Hist.* 4:114 (1837-8).

Boucerosia incarnata (L.f.) N.E.Br., *J. Linn. Soc. Bot.* 17:166(1878).

Caralluma incarnata (L.f.) N.E.Br., *Gard. Chron. Ser.* 3,12: 369 (1892).

Type: South Africa, Cape, Thunberg 6330 (UPS, holo.; K, iso.).

Small to robust succulent forming clump 60-300 mm diam. **Stems** 50-300 mm long, 12-32 mm thick, decumbent, greyish green to purplish green; **tubercles** 3-6 mm long, conical, spreading, joined near bases into 4-5 often somewhat disorganised angles along stem, tipped by sharp yellow tooth, often with 2 stipular denticles on either side near base. **Inflorescences** of 3-10 ± simultaneously opening flowers towards apex of stem; **pedicel** 1-3 mm long, 0.5-1.0 mm thick, holding flower facing ± horizontally; **sepals** 1.5-2.0 mm long, ovate-lanceolate, acute. **Corolla** 7-25 mm diam., campanulate to rotate; outside usually pale pink especially towards tips of lobes and becoming whitish towards base of flower (occasionally yellowish); inside white or cream to pale yellow (to faintly brownish) becoming whitish in tube (whole corolla often turning pale pink before closing), with stiff ascending cylindrical white to pale maroon bristles in mouth of tube and around bases of lobes, otherwise smooth and glabrous; **tube** 1.0-2.5 mm deep, deeply cupular to shallowly bowl-shaped, containing whole column, slightly thickened around mouth; **lobes** (2-) 3-10 mm long, 2.0-2.5 mm broad at base, ascending to spreading, narrowly deltate to lanceolate usually with broader base, folded longitudinally down middle for at least half of length. **Corona** 1.0-1.6 mm tall, 2.0-2.3 mm broad, yellow, sometimes raised on short obtusely pentagonal stipe; **outer lobes** ± 0.5 mm long, ascending to erect, shallowly to deeply bifid into erect deltoid to narrowly deltoid teeth joined laterally to bases of inner lobes and so forming pouch enclosing guide-rails; **inner lobes** < 0.5 mm long, adpressed to backs of anthers and shorter than to slightly exceeding them, ± deltoid to rectangular, obtuse to acute, dorsiventrally flattened, dorsally swollen near base but otherwise without dorsal projection.

Probably, alongside *Q. mammillaris*, *Q. incarnata* is the most typical and frequently encountered species of *Quaqua*. It is mainly a Namaqualand species and is found from Aus in Namibia southwards in South Africa to Bokbaai, which is less than 50 km north of Cape Town. It is mainly found in the hills on and around the coastal plain and in some of the higher mountains of Namaqualand, but not east of them at all, except in a small area north of Calvinia.

The flowers are typically small and cream, produced in small, but often dense clusters along the stems.

Key to the subspecies of *Q. incarnata*

1. Gynostegium seated on short stipe 2.
2. Corolla lobes 3-5 times as long as broad at base **11b. subsp. tentaculata**
2. Corolla lobes 1.5-2.5 times as long as broad at base **11c. subsp. hottentotorum**
1. Gynostegium sessile **11a. subsp. incarnata**

11a. *Quaqua incarnata* subsp. *incarnata*

Piранthus incarnatus var. *albus* G.Don, *Gen. Hist.* 4: 114(1837-8).

Caralluma incarnata var. *alba* (G.Don) N.E.Br., *Fl. Cap.* 4 (1): 882 (1909).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap.* Nov.: t. 34.

Quaqua radiata Plowes, *Excelsa* 16: 89 (1994).

Type: Cape, Vredendal, Plowes 7526 (SRGH).

Stems 15-30 mm diam. **Corolla** 7-12 mm diam., campanulate to nearly rotate; outside pinkish to white at base; inside white to cream, becoming yellow or faintly brownish on lobes with white to pale maroon bristles in mouth of tube and on base of lobes; **tube** 1.0-2.5 mm deep, shallowly bowl-shaped to deeply cupular, sometimes pentagonal; **lobes** 3-6 mm long, 1.5-2.0 mm broad at base, ascending to spreading, deltate to narrowly deltate or parallel-sided, margins slightly reflexed and obtuse apex sometimes incurved. **Corona** 1.0-1.6 mm tall, 2.0-2.3 mm broad, deep yellow, gradually narrowing to base, without stipe.

Distribution and habitat

Quaqua incarnata subsp. *incarnata* is found south of the Knersvlakte from Vredendal and Klawer southwards to near Darling.

Subsp. *incarnata* is found in a wide variety of habitats. Along the coast it is found, usually very sporadically, in the *sandveld* among species of Restionaceae, *Euphorbia burmanii* and other bushes. In the south between St. Helena and Bokbaai it grows on outcrops of granite or limestone, while further inland it is also known on stony patches along the lower slopes of the Nardouw Mountains and the Pakhuis Mountains between Klawer and Clanwilliam. Here it grows among short, karroid bushes and sometimes in patches of taller bush dominated by *Montinia caryophyllacea*.

Diagnostic features and relationships

Plants growing on granite often form robust clumps up to 300 mm across, with particularly stout, conspicuously toothed stems and larger flowers than those that are found further north. Those found in the *sandveld* frequently tend to be smaller and more weakly toothed on the stems and may have very small flowers.

In subsp. *incarnata* the flowers are usually pinkish outside. Inside they are mainly cream on the lobes and this colour tends to white in the tube, but they may be wholly white within. The

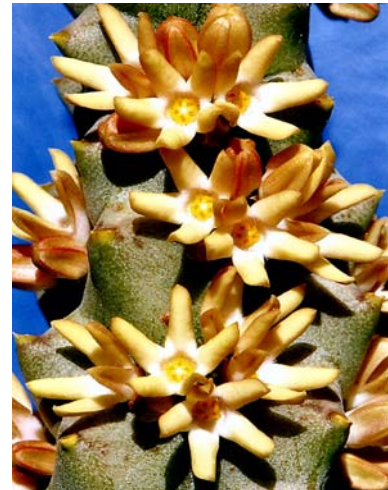


Fig. 13.71. *Q. incarnata* subsp. *incarnata*, PVB, Yserfontein.

mouth of the tube has plenty of small bristles in it. These are usually white but may sometimes be purplish, in which case they serve to emphasise the edge of the tube considerably. The tube varies from relatively shallow and just containing the corona to more than twice as deep as it is tall. There is also considerable variation in the length of the lobes and so the flower as a whole can have quite different shapes. The flowers are often sweetly scented.

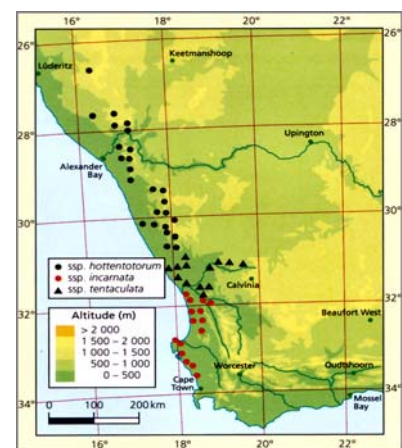


Fig. 13.72. Distribution of *Quaqua incarnata*.

The corona is bright yellow and consists of tiny, deltoid, ascending outer lobules and small inner lobes pressed to the anthers. It is not raised above the base of the tube.

History

Subsp. *incarnata* was one of the first stapeliads that became known to European botanists. It is first figured by Johannes Burman in his *Rare African Plants* (Burman 1738-9). There is evidence to suggest that this drawing was made by Hendrik Claudius during the expedition of the governor Simon van der Stel to Namaqualand in 1685-6 in search of copper. White & Sloane 1937: 1118) or even earlier. In Burman's book the plant is called '*Euphorbia erectum*' and Commelijn (1706) referred it to *Tithymalus* (which is now included in *Euphorbia*). However, in the somewhat earlier plates possessed by Witsen, it was placed in a more reasonable position in *Apocynum*, which here the other known stapeliads were then also considered to belong. It was somehow missed by Linnaeus for his *Species Plantarum* of 1753 and later editions, and was first included in modern binomial listings by his son in 1781 as *Stapelia incarnata*. The description of this name was not based on these early figures, but on a



Fig. 13.73. *Q. incarnata* subsp. *incarnata*, PVB 6351, west of Leipoldtville.

specimen of Thunberg's which may have been collected as early as September 1772, when Thunberg visited Saldanha Bay during his first collecting trip away from Cape Town.



Fig. 13.74. *Q. incarnata* subsp. *incarnata*, PVB 6363, near Lambert's Bay, with relatively flat flowers.



Fig. 13.75. *Q. incarnata* subsp. *incarnata*, PVB 1074, south of Klawer, with especially long corolla tube.

11b. *Quaqua incarnata* subsp. *tentacuiata*

Quaqua incarnata subsp. *tentacuiata* (Bruyns)
Bruyns, *Bot. Jahrb. Syst.* 121: 369 (1999).
Quaqua incarnata subsp. *incarnata* var. *tentacuiata*
Bruyns, *Bradleya* 1: 40 (1983).
Quaqua tentacuiata (Bruyns) Plowes, *Excelsa* 16: 89 (1994).
Type: Cape, 5 miles north-west of Bitterfontein, Bruyns 1666A (NBG).

Stems 12-25 mm diam. **Corolla** 12-25 mm diam., ± rotate; outside uniformly cream to suffused with pink; inside uniformly cream to white, with short adpressed to ascending translucent-white bristles in mouth of tube and on base of lobes inside; **tube** 1.5-2.5 mm deep, cupular, pentagonal; **lobes** 6-10 mm long, 2 mm broad at base, spreading, lowest portion ± deltate from which narrowing and then ± parallel-sided to acute apex, margins strongly reflexed above deltate base. **Corona** 0.8-1.0 mm tall, 1.5-2.0 mm broad, pale yellow, seated on short stipe.

Distribution and habitat

Subsp. *tentacuiata* is found mainly on the Knersvlakte from south of Klawer and around Vredendal northwards to Bitterfontein and Komkans as well as north-eastwards to near the Langeberge north-west of Loeriesfontein. There is a somewhat isolated record from near Kamieskroon. Plants have also been recorded in the hills south-west of Loeriesfontein and sporadically in the valley of the Hantam River due north of Calvinia.

On the Knersvlakte it is particularly associated with the firm, red loam that is found along the Sout River and the lower reaches of the Olifants River. In this area plants usually grow with gregarious species of *Ruschia* such as *R. comptonii* and *R. subsphaerica*, and with

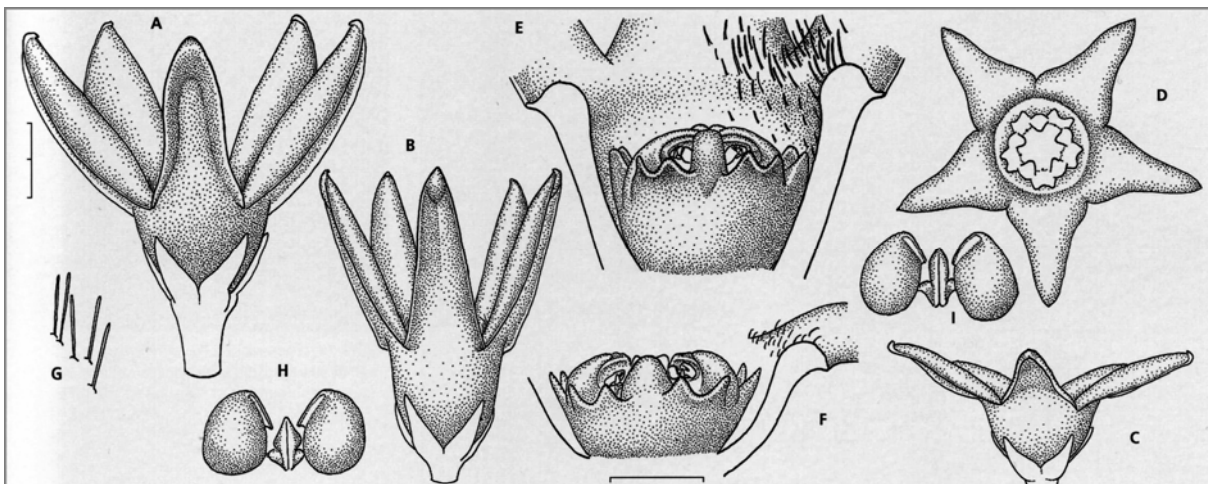


Fig. 13.76. *Quaqua incarnata* subsp. *incarnata*. A, B, C, side view of flower. D, face view of flower. E, F, side view of centre of dissected flower. G, papillae inside corolla in mouth of tube. H, I, pollinarium. Scale bars: A-D, 2 mm (at A); E-F, 1 mm (at F); G, 0.5 mm (at A); H-I, 0.25 mm (at A). Drawn from: A, G, PVB, Yserfontein; B, E, H, PVB, 16 km south of Redelinghuys; C, D, F, I, PVB 6363, near Lamberts Bay.

QUAQUA INCARNATA

Euphorbia muricata. It is also found on gravelly slopes among some of the gneissic hills that penetrate southwards into the Knersvlakte and grows in such spots around Bitterfontein. Further east towards Loeriesfontein it has been observed in stony ground with *Ruschia spinosa* or other small shrubs.

Diagnostic features and relationships

In subsp. *tentacuiata*, although the flowers may be as little as 12 mm across, they are usually quite a bit larger and may even reach 25 mm in diameter. The corolla lobes are tightly folded except right at the base and this makes them long, slender and rather spidery or tentacle-like, which gave rise to the name of this subspecies. The corolla is cream to white both inside and outside when it finally opens, despite being bright green outside often till quite late in its development. The corolla tube is usually pentagonal and is cup-shaped on the outside but, inside, the mouth is distinctly constricted by thickened tissue. Flowers of this subspecies have been observed to emit a weak but unmistakably sweet, honey-like scent.

The corona is indistinguishable from that of subsp. *hottentotorum* and, as in that subspecies, is raised on a stipe above the base of the tube.



Fig. 13.77. *Q. incarnata* subsp. *tentacuiata*, PVB 6145, near Komkans.

Hystory

This subspecies was figured by White & Sloane (1937) under the names *Caralluma incarnata* var. *alba* (fig. 229) and *Caralluma longicuspis* (fig. 329). This was not the correct application of either of these names since the former is

based on Masson's figure (see above), which is of subsp. *incarnata*, and the latter is a synonym of *Orbea lugardii*. It is peculiar that it was not known at all to N.E. Brown (1907-09) and the earliest recorded collection that I have been able to locate was made by Percy Ross Frames in 1931.

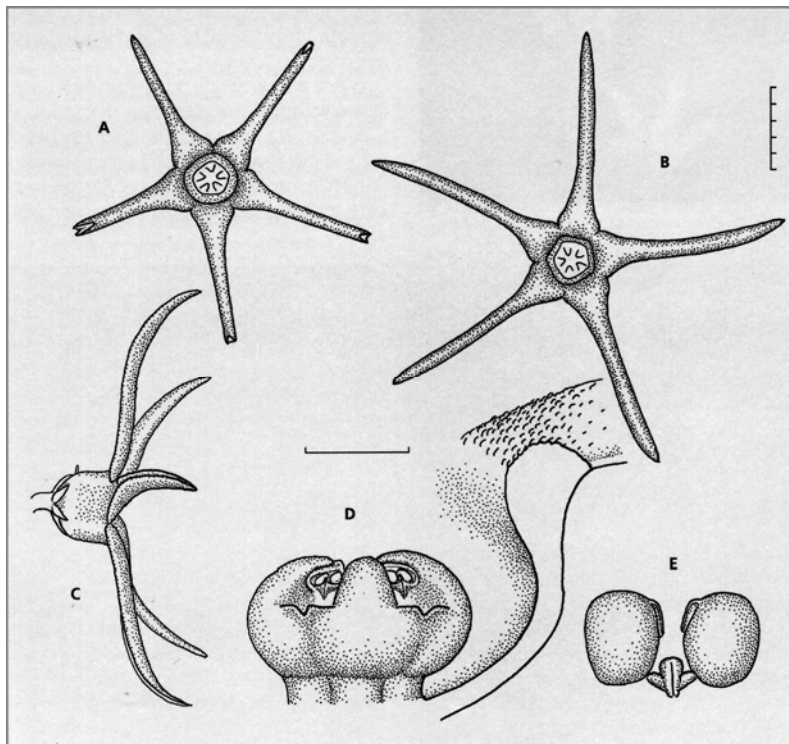


Fig. 13.78. *Quaqua incarnata* subsp. *tentacuiata*. A, B, face view of flower. C, side view of flower. D, side view of gynostegium. E, pollinarium. Scale bars: A-C, 5 mm (at B); D, 1 mm; E, 0.25 mm (at B). Drawn from: A, PVB 6178, south of Vanrhynsdorp; rest, PVB 6375, south of Bitterfontein.



Fig. 13.79. *Q. incarnata* subsp. *tentacuiata*, PVB 6178, south of Vanrhynsdorp, with a small, white spider awaiting visitors on one of the lobes (cf. fig. 4.55).

11c. *Quaqua incarnata* subsp. *hottentotorum*

Quaqua incarnata subsp. *hottentotorum*

(N.E.Br.) Bruyns, *Bot. Jahrb. Syst.* 121: 370 (1999).

Quaqua hottentotorum N.E.Br., *Gard. Chron. N.S.* 12: 8-9 (1879).

Caralluma hottentotorum (N.E.Br.) N.E.Br., *Hooker's Icon. Pl.* 20: sub t. 1903 (1890).

Type: Klipfontein, Namaqualand, Barkly 50 (K).

Caralluma hottentotorum var. *major* N.E.Br., *Fl. Cap.* 4 (1): 881 (1909).

Lectotype: Cape, Mistkraal near Komaggas, *Rich sub N.S. Pillans* 10 (BOL).

Caralluma ausana Dinter & A.Berger, *Feddes Rept. Spec. Nov. Regni Veg.* 15: 354 (1918).

Type: Namibia, near Aus, Dinter 1145 (missing).

Neotype: Namibia, Aus, Dinter 6210 (K, holo.; BOL, iso.).

Caralluma hottentotorum var. *minor* C.A.Lückh. in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1144 (1937).

Lectotype (selected here): White & Sloane, *Stap.*, ed. 2, 3:1144 fig. 248.

Caralluma hottentotorum var. *tubata* C.A.Lückh. in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1144 (1937).

Type: unknown.

Stems 12-20 mm thick. **Corolla** 5-13 mm diam., campanulate; outside cream to pale pink; inside pale yellow with tube white and lobes cream to wholly cream or white (sometimes slightly suffused with green or pinkish), often later becoming pinkish inside and outside before closing, with short skittle-shaped nearly horizontal trans-

parent bristles in mouth of tube and on base of lobes; **tube** 1.2-2.2 mm deep, broadly to shallowly cupular, sometimes pentagonal; **lobes** 2.5-5.5 mm long, $\pm$ 2 mm broad at base, ascending to spreading, narrowly deltate or with deltate base rapidly narrowing to slender upper half, margins slightly to strongly reflexed. **Corona** 0.8-1.0 mm tall, 1.5-2.0 mm broad, pale to deep yellow, seated on short stipe.

Distribution and habitat

The most widely distributed of the three subspecies, subsp. *hottentotorum* is found from Aus in south-western Namibia southwards to Garies in Namaqualand. Apart from a gap between Aus and Witpiitz in Namibia, it is fairly continuously distributed across this region.

Plants are found on the coastal plain and into the gneiss and schist slopes of the western aspect of the escarpment but mostly they remain within the winter-rainfall region and do not advance into the regions of less reliable rainfall to the east of it. They are usually of quite scattered occurrence, sheltering among other succulents and alongside rocks.

Diagnostic features and relationships

In subsp. *hottentotorum* the flowers are generally cream, which sometimes can become slightly darker yellow on the lobes. The corolla lobes vary from a little longer than broad to nearly three times as long as broad and this brings with it much variation in the diameter of the flower so that they are recorded at between 5 and 13 mm across. Usually the lobes spread from the mouth of the tube but occasionally



Fig. 13.80. *Q. incarnata* subsp. *hottentotorum*, PVB 7495, Wildeperdehoek Pass.

they ascend when the flower is fully open and then they give it a quite noticeably campanulate appearance. The tube is also extremely variable, especially in depth: in some flowers it is only just taller than the corona while in others it is over twice as tall. It is often slightly constricted at the mouth, as is the case in subsp. *tentaculata*. Variability in the size of the corolla and the depth of the tube gave rise to several varietal names which have since been abandoned, the

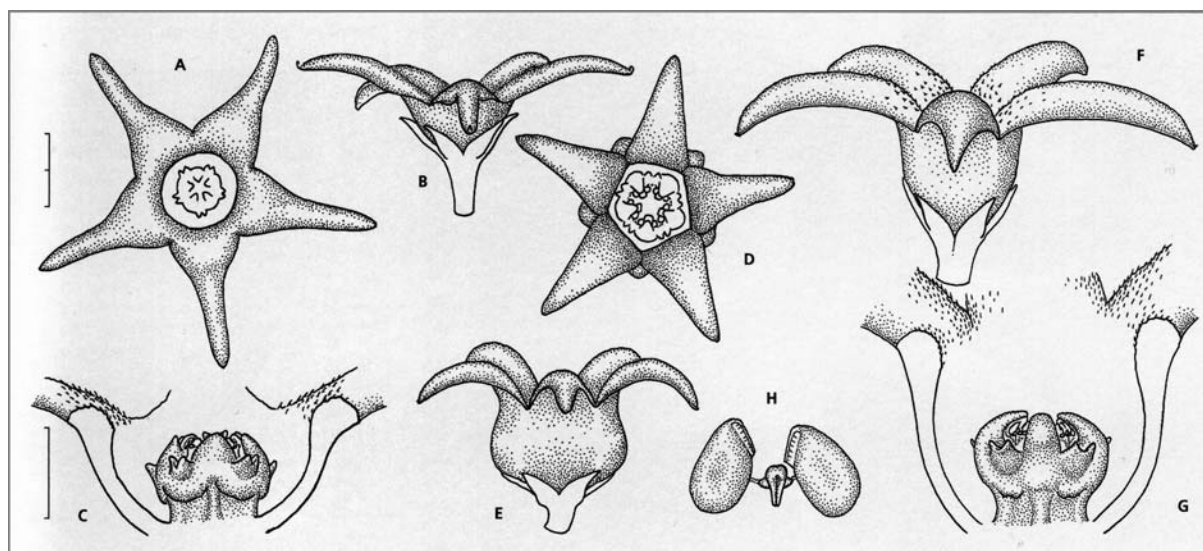


Fig. 13.81. *Quaqua incarnata* subsp. *hottentotorum*. **A, D**, face view of flower. **B, E, F**, side view of flower. **C, G**, side view of dissected flower. **H**, pollinarium. Scale bars: A, B, D-F, 2 mm (at A); C, G, 1 mm (at C); H, 0.25 mm (at A). Drawn from: A-C, PVB 4193, Rosyntjie Mountain; D, E, *P. Desmet*, between Port Nolloth and Holgat (no specimen); F-H, *Kratz*, Pockenbank, Namibia.

QUAQUA FRAMESII

plants involved being part of a much wider pattern of variability which does not seem to be geographically linked at all. Flowers of this subspecies have sometimes been noted to emit a very sweet scent for a short time after opening.

The corona is seated at the foot of the tube on a short stipe and it is usually (but not always) well separated from the sides of the tube. The whole structure is pale to deep yellow. The outer lobes are often minute and somewhat pouch-like with a slight notch at their apices, but they may also consist of pairs of small delto-lobules as in subsp. *incarnata*.

History

'*Quaqua hottentotorum*' was described from material collected at Klipfontein, near Steinkopf in Namaqualand, and sent to Kew by Henry Barkly. The first plant flowered at Kew in September 1875. N.E. Brown first placed this species in a separate genus, *Quaqua*, but he later considered it better to place it in *Caralluma*. Today this taxon is viewed as part of a much broader range of forms that are all included in *Quaqua incarnata*.



Fig. 13.82. *Q. incarnata* subsp. *hottentotorum*, PVB 6767a, near Garies.



Fig. 13.83. *Q. incarnata* subsp. *hottentotorum*, PVB 5208, Sonberg, Namibia.

12. Quaqua framesii

Quaqua framesii (Pillans) Bruyns, *Bradleya* 1: 43 (1983).

Caralluma framesii Pillans, *S. African Gard. & Country Life* 18: 62 (1928, special reprint).

Type: South Africa, Cape, Vanrhynsdorp, Ross
Frames sub NBG 1212/26 (BOL, holo.; K, iso.).

Small to robust succulent forming dense clump 60-500 mm diam. **Stems** 50-200 mm long, 15-25 mm thick, decumbent, grey-green to somewhat purplish; **tubercles** 3-6 mm long, conical, spreading, joined near bases into 4-5 often slightly spiralling or disorganised angles along stem, tipped with sharp hardened yellow tooth slightly flattened above, often with 2 denticles near base. **Inflorescences** of 3-10 ± simultaneously opening flowers towards apex of stem; **pedicel** 1-3 mm long, 1 mm thick, spreading and holding flower facing horizontally; **sepals** 2.0-2.5 mm long, ovate-lanceolate, acute. **Corolla** 11-18 mm diam., rotate to campanulate; outside yellow-green occasionally with slight pinkish tinge; inside bright yellow or greenish yellow on lobes becoming paler towards mouth of tube, around mouth of tube and base of lobes with stiff cylindrical translucent-white ascending bristles each arising from a low papilla, otherwise smooth; **tube** cupular to conical, 1.8-2.2 mm long, 2-3 mm diameter at mouth inside; **lobes** 7-8 mm long, 2 mm broad at base, ascending to spreading, ± uniform in width to obtuse slightly incurved apex, longitudinally folded back so upper surface convex. **Corona** 1.8-2.0 mm tall, ± 2 mm broad, pentagonal when viewed from above with vertices formed by lower part of outer lobes, bright yellow, sessile or raised on only very short stipe; **outer lobes** ± 1 mm long, bifid but only very slightly with lobules remaining connivent and nearly completely closing nectarial orifice, lower down forming deep pouch between bases of inner lobes; **inner lobes** ± 0.5 mm long, adpressed to backs of anthers but not usually exceeding them, ± rectangular and broadening towards truncate often emarginate apex, dorsiventrally flattened, sometimes hispid towards dorsally slightly swollen base.

Distribution and habitat

Quaqua framesii is one of two localised members of the genus which grow on the Knersvlakte in southern Namaqualand. It is found in a small area of the southern Knersvlakte mainly to the west of the main road from Vanrhynsdorp to

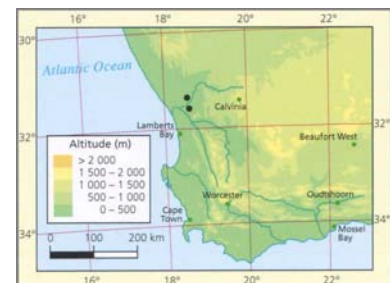


Fig. 13.84. Distribution of *Quaqua framesii*.



Fig. 13.85. *Q. framesii*, PVB 1451, north of Vredendal.

Nuwerus, north of the Olifants River and more or less following the course of the Sout River.

Quaqua framesii grows among short bushes and especially among and inside tufts of the extremely spiny grass *Cladoraphis spinosa* in red sand, where this has become somewhat stabilised. It has also been seen on stony ground among *Ruschia* shrublets, for example, on the Rooiberg. On several occasions it has been collected together with *Q. incarnata* subsp. *tentaculata*.

Diagnostic features and relationships

Plants of *Q. framesii* can be very large, reaching up to 500 mm in diameter, and they have robust stems with rather prickly teeth on the tubercles, usually with two small, but quite obvious stipular denticles on either side of each tooth. In these details and in their robustness, they bear some resemblance to the robust forms of *Q. incarnata* found on granites around Saldanha.

Flowers are produced in many small clusters near the tips of the stems and often all those on a cluster will open more or less simultaneously. The buds are usually greenish but the flower, when it opens, is a bright yellow, becoming paler around the mouth of the



Fig. 13.86. *Q. framesii*, PVB 1451, north of Vredendal, in habitat, July 1977.

tube and inside it. The corolla lobes are more or less uniformly broad right to their tips and the tips are generally somewhat incurved. In the centre there is a small, but relatively deep tube whose mouth is very slightly constricted by a ring of white bristles. The tube is just deep enough to contain the whole of the bright yellow gynostegium.

Quaqua framesii is closely related to *Q. incarnata*, as can readily be seen from the yellow colour of the flowers, the bristles in the mouth of the tube, the somewhat similarly shaped gynostegium and from the similar-looking stems. Also the more or less uniform width of the corolla lobes most of the way to their tips (which are incurved) and the rather longer bristles in the mouth of the tube suggest that it is to subsp. *incarnata* that *Q. framesii* is most closely allied. However, from *Q. incarnata* it can be separated by several unusual features of

the gynostegium. The lower parts of the outer corona lobe form a deep pouch leading nearly to the base of the gynostegium and it is these pouches that give the gynostegium its usually pentagonal shape when viewed from above. Furthermore, the outer corona lobes are only very slightly bifid at the apices and the lobules remain connivent rather than diverging, as is usually the case in *Q. incarnata*.

History

Quaqua framesii was one of the various interesting discoveries of Percy Ross Frames, who collected it in 1926 near Vanrhynsdorp. At a spot near Vredendal, where several plants were first observed in June 1975, some were still present in July 2004, although many individuals had succumbed to the droughts of the last few years.

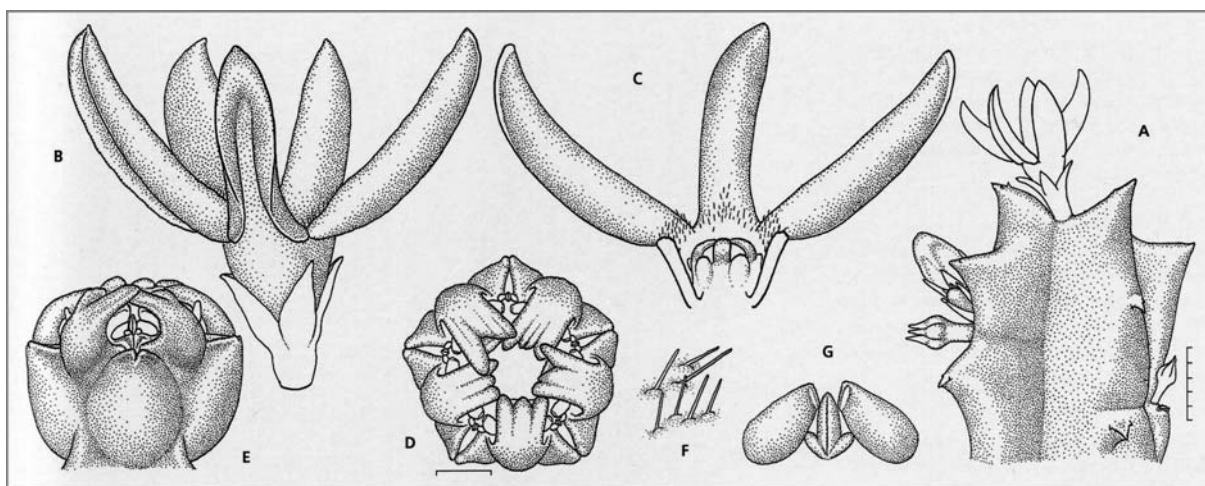


Fig. 13.87. *Quaqua framesii*. A, apex of stem with flowers. B, side view of flower. C, side view of dissected flower. D, face view of gynostegium. E, side view of gynostegium. F, papillae inside corolla in mouth of tube. G, pollinarium. Scale bars: A, 5 mm; B-C, 2 mm (at A); D, E, 0.5 mm (at D); F, 0.5 mm (at A); G, 0.25 mm (at A). Drawn from PVB north of Vanrhynsdorp.

QUAQUA ARMATA

13. *Quaqua armata*

Quaqua armata (N.E.Br.) Bruyns, *Bradleya* 1: 65 (1983).

Caralluma armata N.E.Br., *Hooker's Icon. PL* 20: t. 1902 (1890).

Sarcophagophilus amatus (N.E.Br.) Dinter, *Feddes Rept. Spec. Nov. Regni Veg. Beih.* 53:108 (1928).

Type: South Africa, Cape, at foot of Kamiesberg, *Barkly* 47 (K).

The two species *Q. arenicola* and *Q. armata* are fairly similar. Both have a clump-forming habit with the side-stems rooting readily at their bases, which is an unusual feature among these more robust, relatively large-flowered taxa.

In *Q. arenicola*, which has a more easterly distribution on the edge of the winter-rainfall region and the western margin of the Great Karoo, the spreading tubercles on the stems are arranged fairly exactly into four neat tiers, the stems are uniformly grey- to purple-green and the leaf-rudiment may be subtended by a pair of stipular denticles surrounded by a few 'hairs'. The flowers are borne on peduncular patches at more or less any height on the stems but with a preponderance towards the base.

In *Q. armata*, which occurs along the west coast in Namaqualand, the spreading tubercles on the stem are rather untidily arranged into four or five irregular rows, the stems are brightly mottled with purple to blackish on a grey to green background and the leaf-rudiment is mainly without stipular denticles and without hairs. The flowers are borne mainly towards the apex of the stems.

Both subspecies of *Q. armata* occur with *Q. mammillaris* on occasion. The two species can be separated by the much more aggressively spiky tubercles of *Q. mammillaris* that are attenuated into a sharp spike, as opposed to those of *Q. armata* which are not quite as dense on the stem and are always somewhat blunter, not being as sharply hardened at their tips. The corolla lobes are also very much more slenderly acuminate in *Q. mammillaris*, whereas in *Q. armata* the lobes are acute and taper far less gradually to their tips.

Succulent forming broad spreading clump up to 0.5 m diam. or more, rooting freely near bases of side-branches. **Stems** 50-200 mm long, 15-30 mm thick, decumbent, grey-green mottled with purple; **tubercles** 3-15 mm long, deltoid, conical to laterally flattened, spreading to descending, arranged loosely into 4-5 angles along stem (not always clearly into angles), each tipped with

blunt to sharp grey to yellow and hardened tooth, mostly without stipules. **Inflorescences** of 3-10 ± simultaneously opening flowers towards apex of stem; **pedicel** 1-2 mm long, 0.75-2.00 mm thick, ascending to spreading with flowers mainly facing horizontally; **sepals** 1.5-2.5 mm long, 1 mm broad at base, pale green, ovate-lanceolate, acuminate, adpressed to corolla. **Corolla** 8.0-28.5 mm diam., campanulate (rarely rotate); outside uniformly pale yellow to purple-red or maroon on lobes changing to pale green to white speckled with purple-brown towards base; inside tube usually cream or white sometimes with bands of dark purple on white, mouth of tube and lobes speckled with purple-brown on yellow to uniformly dark purple-black, sometimes with upward-pointing bristles in mouth of tube and on base of lobes, otherwise glabrous and smooth; **tube** 2.0-5.5 mm long and ± as broad at mouth, broadly to deeply cupular, corolla thickened around mouth; **lobes** 6-15 mm long, 3.5-4.5 mm broad at base, ascending to spreading, tapering from base to acute apex (rarely narrowing abruptly at apex to acute tip), folded longitudinally along middle so that upper surface often keeled. **Corona** 2.3-3.0 mm diam., purple- or red-brown or purple-black becoming yellow towards base, raised on very short stipe; **outer lobes** ± 0.5-1.0 mm long, erect, shallowly to deeply bifid into erect deltoid lobules, laterally fused to bases of inner lobes to form deep pouch around guide-rails; **inner lobes** ± 0.5 mm long, adpressed to backs of and usually exceeding anthers, rectangular, truncate to emarginate, dorsiventrally flattened, with erect deltoid or truncate ridge-like or low and rounded dorsal projection in series with outer lobes.

13a. *Quaqua armata* subsp. *armata*

Corolla 10-20 mm diam.; outside speckled with purple to pale yellow; inside varying from yellow to cream with fine brownish spots becoming denser towards tips of lobes and in tube, to spotted with red on white in tube with dark purple-brown lobes, devoid of papillae; **lobes** 6.5-14.0 mm long, 4.0-4.5 mm broad at base, margins folded back down middle in upper half to two thirds, tapering gradually from base to acute tip. **Corona** 2.6-3.0 mm diam., purple- to red-brown above, lower half bright yellow; **inner lobes** with truncate ridge-like dorsal projection.

Distribution and habitat

Subsp. *armata* is quite common and widely distributed in the lowlands of Namaqualand from Papendorp northwards to around Wallekraal and inland further northwards to the lower levels of the Wildeperdehoek Pass.

Plants are found mostly among rocks on gravelly slopes on low gneiss hills or on firm red loam. They grow usually with various species of creeping and low shrubby succulent Aizoaceae (especially *Cephalophyllum*). It apparently does not occur in the sandveld on the looser, red sands that are found further west.

Diagnostic features and relationships

Specimens of subsp. *armata* form spreading, diffuse clumps which root freely on many of the stems. The stems are stout and usually mottled with purple on a greyish green background. They have prominent, conical tubercles with a blunt tip and are without any trace of stipular denticles.

Key to the subspecies of *Q. armata*

- | | |
|--|-----------------------------|
| Corolla inside glabrous | 13a. subsp. <i>armata</i> |
| Corolla inside papillate at least in mouth of tube | 13b. subsp. <i>maritima</i> |

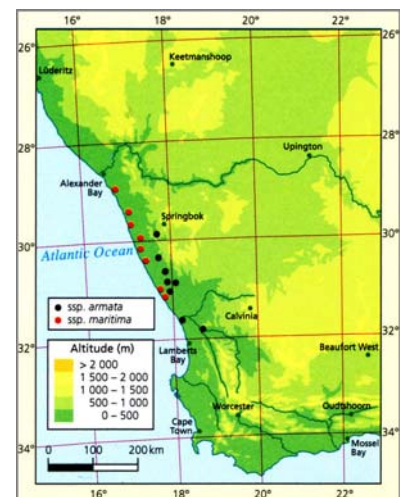


Fig. 13.88. Distribution of *Quaqua armata*.

The flowers arise in dense clusters towards the tips of the stems. They are relatively large but are not always able to open out fully because of the congestion that occurs in the inflorescences. In this subspecies, the inside of the corolla has been found to be particularly variable in colour. The most striking ones have a yellow background which is faintly and finely speckled with brown. In these, the spots become more dense in the tube and towards the tips of the lobes so that the colour is darker in these areas. From this colour they vary to pale brown or dark purple-brown on the lobes with red spots on a white background in the tube. The inside of the corolla is without any of the raised bristle-tipped papillae that are common in most of the other larger-flowered species. The corolla tube is generally comparatively broad but it is a good deal longer than the broad and flattish gynostegium.

On the gynostegium, the outer corona lobes are organised into a cup-like structure and the small inner lobes are incumbent on the anthers, with a truncate, ridge-like dorsal projection. These dorsal ridges are often confluent with, and not distinguishable at all from the outer lobes. In such cases they appear to form an integral part of the cupular outer series but they may also be quite separate from them.

History

Subsp. *armata* was one of the plants sent by Henry Barkly to N.E. Brown at Kew during the period 1870-7 when Barkly was governor of the British colony at the Cape of Good Hope. Barkly's material came from somewhere at the foot of the Kamiesberg in Namaqualand. It was later found again by N.S. Pillans near Wallekraal in October 1924.



Fig. 13.89. *Q. armata* subsp. *armata*, PVB 1646, near Kotzesrus.



Fig. 13.90. *Q. armata* subsp. *armata*, PVB 3840, southeast of Wallekraal.



Fig. 13.91. *Q. armata* subsp. *armata*, PVB 1471, Wildeperdehoek Pass.

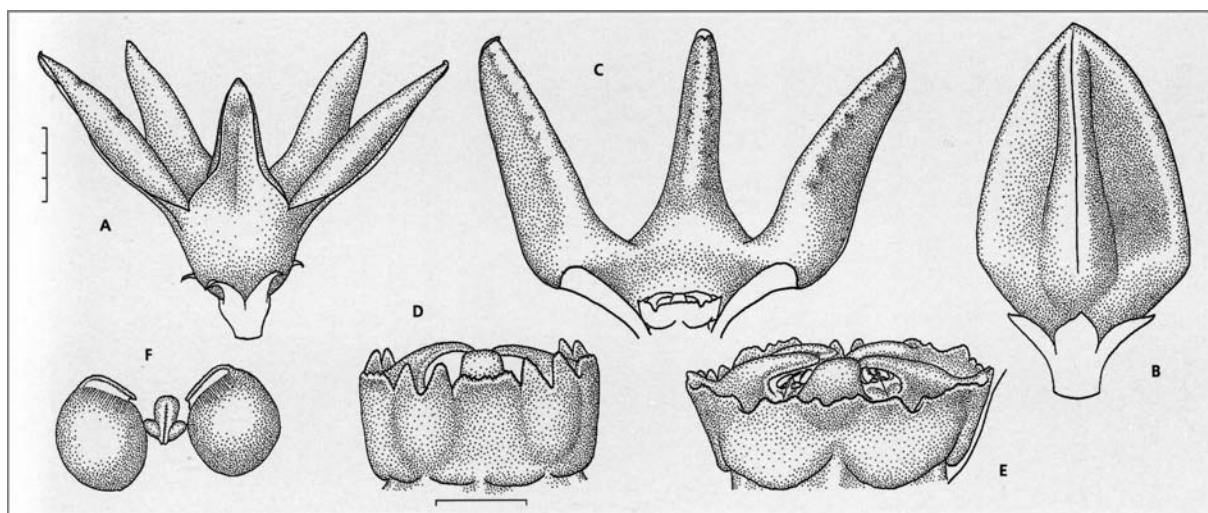


Fig. 13.92. *Quaqua armata* subsp. *armata*. A, side view of flower. B, bud. C, side view of dissected flower. D, E, side view of gynostegium. F, pollinarium. Scale bars: A-C, 3 mm (at A); D-E, 1 mm (at D); F, 0.25 mm (at A). Drawn from: A, B, D, F, PVB 1471, Wildeperdehoek Pass; C, E, PVB 6154, near Kotzesrus.

QUAQUA ARMATA

13b. *Quaqua armata* subsp. *maritima*

Quaqua armata subsp. *maritima* Bruyns, *Bradleya* 1:66 (1983).

Quaqua maritima (Bruyns) Plowes, *Excelsa* 16: 97 (1994).

Type: Cape, Hondeklip Bay, Bruyns 1457 (NBG).

Corolla 9-18 mm diam.; outside dark purple-red changing to green towards base; inside often slightly rugulose, velvety maroon to purple-black on lobes and mouth of tube with cream to white in tube where sometimes with maroon rings or bars and spots, with numerous papillae around base of lobes and in corolla tube each tipped with an ascending bristle; **lobes** 5-8 mm long, 2-4 mm broad at base, strongly folded back down middle, tapering gradually from base to acute tip to narrowing only near end to obtuse tip. **Corona** 2.3-3.0 mm diam., purple-black becoming yellow towards base; **inner lobes** with $\pm$ pyramidal to obtuse dorsal projection ranging from larger than outer lobules to absent.

Distribution and habitat

Subsp. *maritima* is known from the narrow, coastal strip of Namaqualand from the Holgat River south of Alexander Bay to some 30 km north of the mouth of the Olifants River in the *sandveld*. Large parts of this region are covered with loose, red to grey sands. On these sands the vegetation varies between an arid *fynbos* dominated by Restionaceae (for example, west of Komaggas) and one almost totally dominated by succulents. Dotted within these sandy regions are many, often very small patches of harder, loamy ground supporting a karroid vegetation which mainly consists of small succulents.

Q. armata subsp. *maritima* is found both in the loose sands and on the harder, karroid patches but is much more regularly



Fig. 13.93. *Q. armata* subsp. *maritima*, PVB 9874, near Holgat River, in habitat, June 2004.

encountered in sand. Here plants start off underneath another shrub, but they often outlive it and then grow fully in the open. They are usually of extremely scattered occurrence in the sandy areas.

Diagnostic features and relationships

In subsp. *maritima* the stems may be stout and attractively mottled with purple as in subsp. *armata*. However, they may also be rather more slender, with smaller tubercles and a somewhat less obvious mottling. In such cases the tooth on each tubercle may be quite small and it may even have a pair of stipular denticles near the base.

The flowers in this subspecies are usually

smaller than in subsp. *armata* and this is especially so in the southern portion of its distribution to the west of Bitterfontein. They usually emit an unpleasant odour of excrement. On the outside they are usually somewhat shiny. Inside, the corolla has a velvety texture. The lobes are dark purple-black to maroon and this colour changes to cream in the tube where there is also sometimes a ring or a series of concentric bars of maroon or there may be many maroon spots. In subsp. *maritima* there is a crust of bristle-tipped papillae around the mouth of the tube and on the bases of the lobes. The lobes are particularly variable in shape and may be anything from tapering gradually to an acute point to narrowing abruptly to an almost obtuse tip.

The gynostegium is slightly less broad than

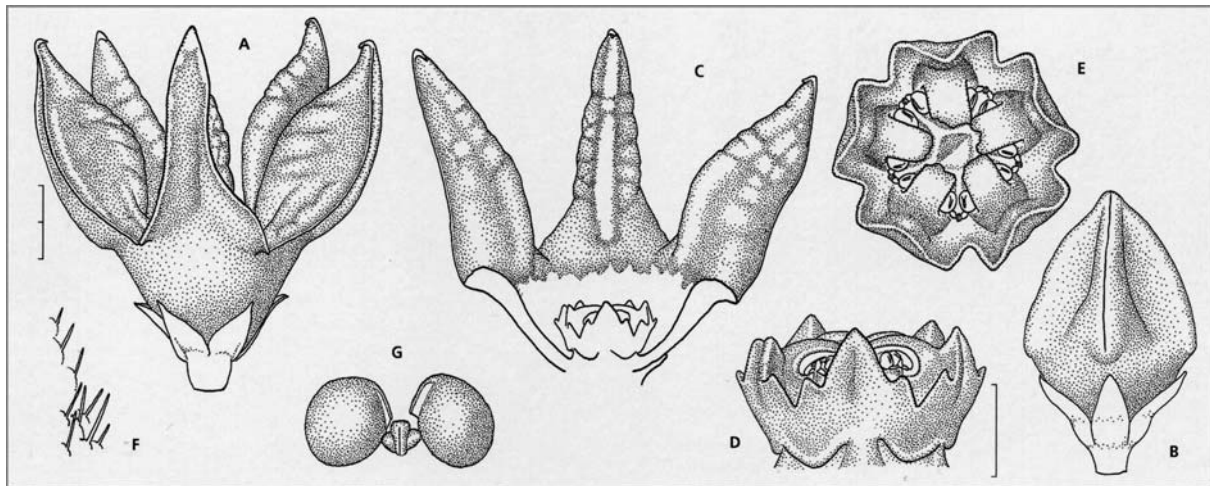


Fig. 13.94. *Quaqua armata* subsp. *maritima*. A, side view of flower. B, bud. C, side view of dissected flower. D, side view of gynostegium. E, face view of gynostegium. F, papillae inside corolla in mouth of tube. G, pollinarium. Scale bars: A-C, 2 mm (at A); D, E, 1 mm (at D); F, 0.5 mm (at A); G, 0.25 mm (at A). Drawn from PVB 3851, north-west of Wallekraal.

in subsp. *armata* and usually sits more isolated in the base of the tube. The outer lobes are much as in subsp. *armata* but the inner lobes often have a relatively tall dorsal projection which may be taller than the outer lobes. However, as is usual, this is variable and they have been seen from this size to almost absent.

History

The discovery of subsp. *maritima* must be credited to N.S. Pillans, who collected it in October 1924 between Riethuis and Hondeklip Bay apparently for the first time. It has been rarely recorded and seems to have been observed for the second time in May 1939, at the Holgat River south of Alexander Bay. On this occasion it was collected by J.P. Roux.

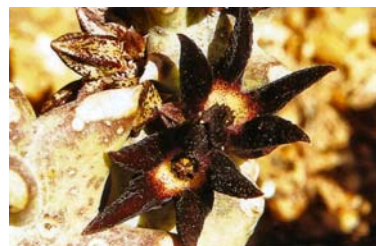


Fig. 13.95. *Q. armata* subsp. *maritima*, PVB 6735, west of Wallekraal.



Fig. 13.96. *Q. armata* subsp. *maritima*, PVB 6756, west of Komaggas, June 2004.



Fig. 13.97. *Q. armata* subsp. *maritima*, PVB 6157, west of Bitterfontein.



Fig. 13.98. *Q. armata* subsp. *maritima*, PVB 6720, west of Bitterfontein.

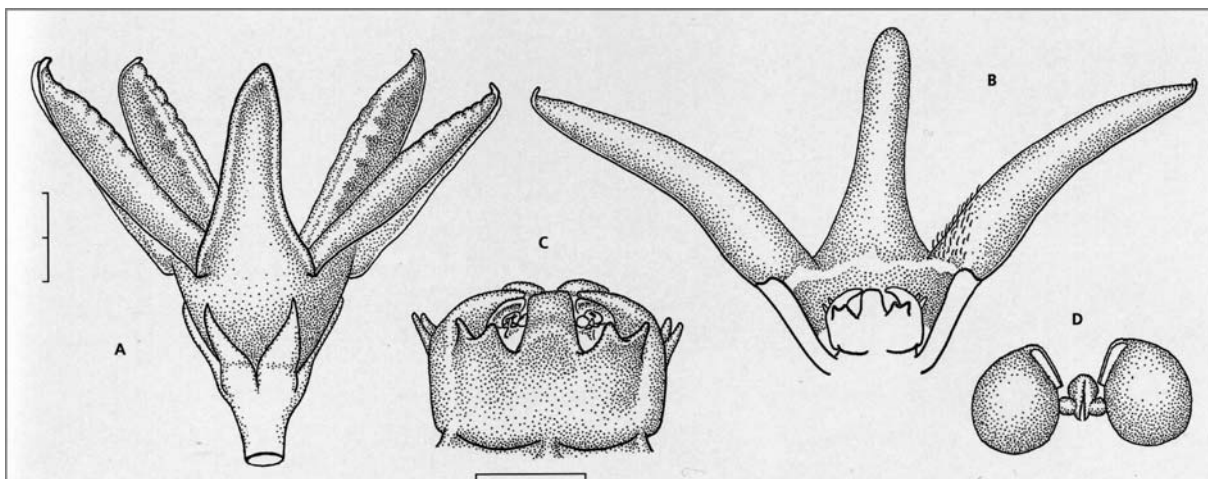


Fig. 13.99. *Quaqua armata* subsp. *maritima*, small-flowered forms from the southern end of the distribution. A, side view of flower. B, side view of dissected flower. C, side view of gynostegium. D, pollinarium. Scale bars: A, B, 2 mm (at A); C, 1 mm; D, 0.25 mm (at A). Drawn from PVB 6157, A from a different plant to the rest, west of Bitterfontein.

QUAQUA MULTIFLORA

14. *Quaqua multiflora*

Quaqua multiflora (R.A.Dyer) Bruyns, *Bradleya* 1:68(1983).

Caralluma multiflora R.A.Dyer, *Bothalia* 12: 253 (1977).

Type: South Africa, Cape, west of Rebusie, Calvinia, Hanekom 2475 (PRE, holo.; K, iso.).

Succulent forming broad spreading clump up to 0.5 m diam. or more, often rooting freely near bases of side-branches. **Stems** 50-200 mm long, 20-30 mm thick, decumbent, bluish green often mottled with purple to purplish mottled with darker purple; **tubercles** 4-15 mm long, conical to laterally flattened, spreading, somewhat irregularly joined into 4 or 5 angles along stems, each tipped with sharp hardened tooth. **Inflorescences** of 3-30 ± simultaneously opening flowers usually in upper half of stem; **pedicel** 2-5 mm long, 1.5 mm thick, spreading and holding flower facing horizontally; **sepals** 2-3 mm long, ovate to linear-lanceolate, acute. **Corolla** 15-18 mm long, tubular-campanulate, in bud usually distinctly oblong and widening from mouth of tube towards apex; outside shiny dark purple-black to purple-red on lobes changing to white blotched with purple-black on tube; inside uniformly purple-black to purple-red on lobes becoming blotched on yellow background in lower half of lobes or around mouth of tube, white or pale yellow with few dark dots in tube, with conical obtuse white to dark purple papillae around mouth of tube and for some distance outwards along middle of lobe, papillae often aggregated into partially fused clusters and each tipped with an ascending bristle; **tube** 2.3-4.0 mm long, 3.0-3.3 mm broad at mouth, cupular, narrowing ± from middle towards somewhat thickened

mouth; **lobes** 12-14 mm long, ± 3 mm broad at base, erect to slightly spreading, usually constricted above base and then linear and parallel-sided or widening gradually to incurved ± deltoid-acute tip, longitudinally folded back except at tip and towards base so that upper surface distinctly keeled. **Corona** 2.7-3.0 mm tall, 2.5-2.7 mm broad, with purple lobes and cream to white base, raised on very short stipe; **outer lobes** 0.5-1.0 mm long, erect, bifid into ascending to erect deltoid to deltoid-lanceolate teeth, fused laterally with bases of inner lobes to form deep pouch; **inner lobes** 1-2 mm long, adpressed to backs of anthers and exceeding them, then connivent-erect and rising into column in centre, linear, obtuse, dorsiventrally flattened, with slightly spreading deltoid to truncate dorsal projection in series with outer lobes.

Distribution and habitat

Quaqua multiflora is known to occur over a relatively wide area towards the eastern edge of the winter-rainfall region. It is known from a few places around Matjiesfontein, then roughly 200 km to the north at several localities north-east, south and south-east of Calvinia. Recently I located a further, quite substantial colony a little south of Leliefontein in the Kamiesberg, about 200 km to the north-west of Calvinia, and a few specimens were also found east of Springbok. This remarkably disjointed distribution is similar to that of *Adromischus phillipsiae* (Bruyns 1998a) and, as in this species (which

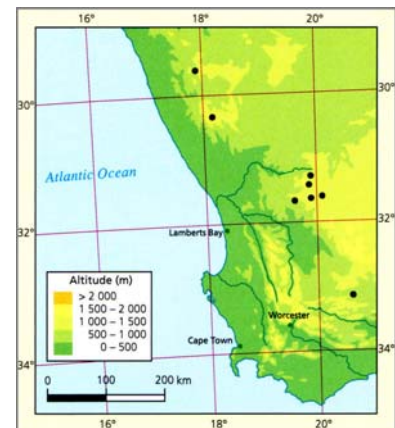


Fig. 13.100. Distribution of *Quaqua multiflora*.

has quite stringent requirements of habitat), this patchiness in the distribution appears to be real rather than a consequence of inadequate collecting.

Plants are generally found on gentle shale or gneiss slopes or in flats among bushes of *Eriocephalus* or *Pteronia incana*.

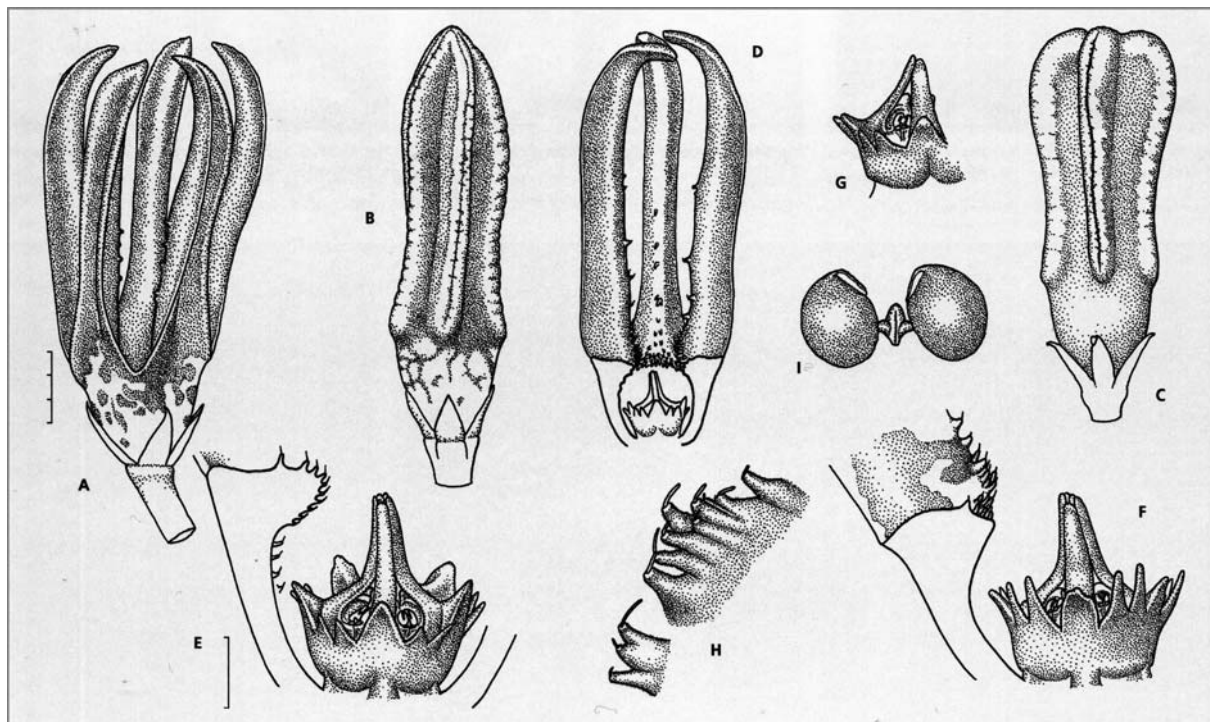


Fig. 13.101. *Quaqua multiflora*. A, side view of flower. B, C, bud. D, side view of dissected flower. E, F, G, side view of gynostegium. H, papillae inside corolla just above mouth of tube. I, pollinarium. Scale bars: A-D, 3 mm (at A); E-G, 1 mm (at E); H, 0.5 mm (at E); I, 0.25 mm (at E). Drawn from: A, B, D, E, H, I, PVB 1224, north of Matjiesfontein; C, G, PVB 4297, south-east of Calvinia; F, PVB 5341, south of Leliefontein, Kamiesberg.

Diagnostic features and relationships

This species has stout often quite attractively mottled stems which form substantial clumps up to 0.5 m in diameter. The tubercles are also stout and tipped with a hard and often quite sharp tooth. Their somewhat disorganised arrangement on the stems makes it easily separable from *Q. arenicola*. However, it is not so readily distinguished vegetatively from *Q. armata*, and the plants can look very similar. One very large plant of *Q. multiflora* seen south-east of Calvinia (PVB 4297) had longer stems than usual and looked similar to *Q. mammillaris*. Here only the more spreading habit and the roots that were produced on a few of the side-branches suggested its real identity, which was confirmed once flowers appeared.

In *Q. multiflora* the flowers are produced in dense clusters of up to 30 per inflorescence towards the tips of the stems. Most of the flowers in a cluster open more or less simultaneously. From the point of view of the colour of the inside, these flowers are similar to most of the larger-flowered species. They have the typically dark, often purple-black lobes and whitish tube with a few dark spots mainly near the mouth which are found in most of them. They also emit an unpleasant odour. Very occasionally the dark colour of the lobes is speckled with yellow but usually their dark colour only begins to break up towards the mouth of the tube. The outside

is smooth and often rather shiny but the inside is velvety and covered, or rather 'encrusted', around the mouth of the tube with a growth of quite large papillae. From all the similar species *Q. multiflora* is easily distinguished by the shape of the corolla lobes, which are either parallel-sided or widen gradually to a broader, abruptly acute, incurved tip. This shape in the lobes can usually be detected in the buds which, instead of narrowing from the base of the lobes towards the apex, are somewhat club-shaped.

The corona is usually purplish towards the tips of the lobes and white lower down. The outer lobes are each bifid into small, deltoid, erect teeth and these, together with the similarly shaped dorsal ridge on the inner lobes, form a cup-like structure. The inner lobes are quite long. Initially they are pressed to the anthers, after which they rise in the centre into a slender column which nearly reaches the mouth of the tube.

History

Quaqua multiflora was described from material collected by Willem J. Hanekom just west of Calvinia in 1975 and first observed at this locality in August 1974. Dyer (1977) mentioned that, according to his enquiries, there appeared to be no other records of the species. However, the first record of *Q. multiflora* seems to have been made by Wynand J. Louw, who collected it near Matjiesfontein in November 1935 (PRE)



Fig. 13.102. *Q. multiflora*, PVB 4297, south-east of Calvinia.



Fig. 13.103. *Q. multiflora*, PVB 1224, north of Matjiesfontein, in habitat, October 1991.

and it was also collected south-east of Calvinia as early as 1953 by H. Hall. A few more localities for it have been discovered recently, including one in the Kamiesberg and one which was found in August 2000 near Springbok. Both of these new records have extended the known distribution significantly to the north.



Fig. 13.104. *Q. multiflora*, PVB 5341, south of Leliefontein, Kamiesberg, with corolla lobes mottled to near their tips.

QUAQUA ARENICOLA

15. *Quaqua arenicola*

Quaqua arenicola (N.E.Br.) Plowes, *Excelsa* 16: 98 (1994).

Caralluma arenicola N.E.Br., *Fl. Cap.* 4 (1): 883 (1909).
Quaqua armata subsp. *arenicola* (N.E.Br.) Bruyns, *Bradleya* 1: 67 (1983).

Type: South Africa, Cape, near Matjiesfontein, N.S. *Pillans* 44 (K, holo.: BOL, iso.).

Succulent forming dense and often robust clump 150-500 mm diam. **Stems** 20-150 mm long, 15-25 mm thick, decumbent to erect, uniformly green to grey-purple; **tubercles** 5-10 mm long, conical, spreading, joined in lower half into 4 angles along stem, each tipped with sharp hardened yellow tooth usually somewhat flattened above and with 2 stipular denticles on either side. **Inflorescences** of 3-20 ± simultaneously opening flowers mostly in lower (to upper) half of stem; **pedicels** 2-5 mm long, 1.0-1.5 mm thick, ascending to spreading; **sepals** 4 mm long, 1 mm broad at base, whitish flecked with red. **Corolla** 15-30 mm diam., campanulate to rotate; outside dark purple-red changing to pale green speckled with purple-red on tube; inside velvety to dull dark purple-red to purple-black on lobes and into mouth of tube, below this mottled and banded with same dark colour on cream, with low obtuse papillae each tipped by a short ascending bristle at least in mouth of tube; **tube** 2-4 mm long, 3-5 mm broad at mouth, cupular, with corolla thickened at mouth; **lobes** 7.5-15.0 mm long, 3.5-1.0 mm broad at base, ascending

Key to the subspecies of *Q. arenicola*

Corolla papillate within and around mouth of tube only **15a. subsp. *arenicola***
Corolla papillate over entire inner face **15b. subsp. *pilifera***

to spreading, narrowly lanceolate, acute, margins folded back so that upper surface convex. **Corona** 1.2-2.0 mm tall, 2-3 mm broad, yellow to reddish purple, raised on stipe up to 0.5 mm long; **outer lobes** ± 1 mm long, erect, shallowly bifid into erect obtuse deltoid lobules, laterally

fused in lower half to bases of inner lobes to form deep pouch; **inner lobes** 0.5-1.0 mm long, adpressed to backs of anthers and equalling them, ± rectangular, dorsiventrally flattened, with obtuse swollen dorsal projection in series with outer lobes.

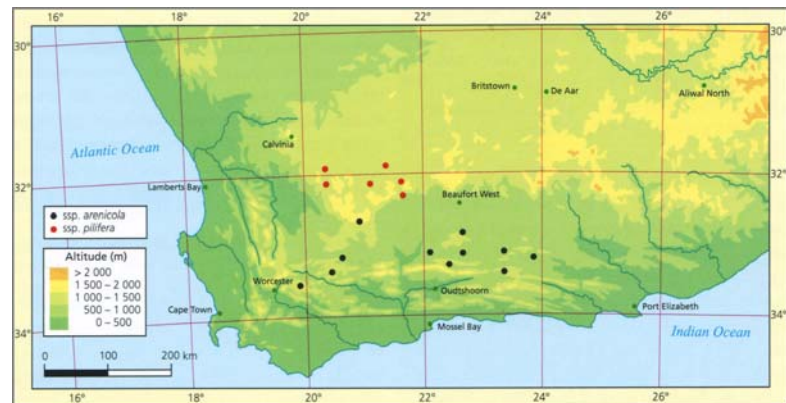


Fig. 13.105. Distribution of *Quaqua arenicola*.

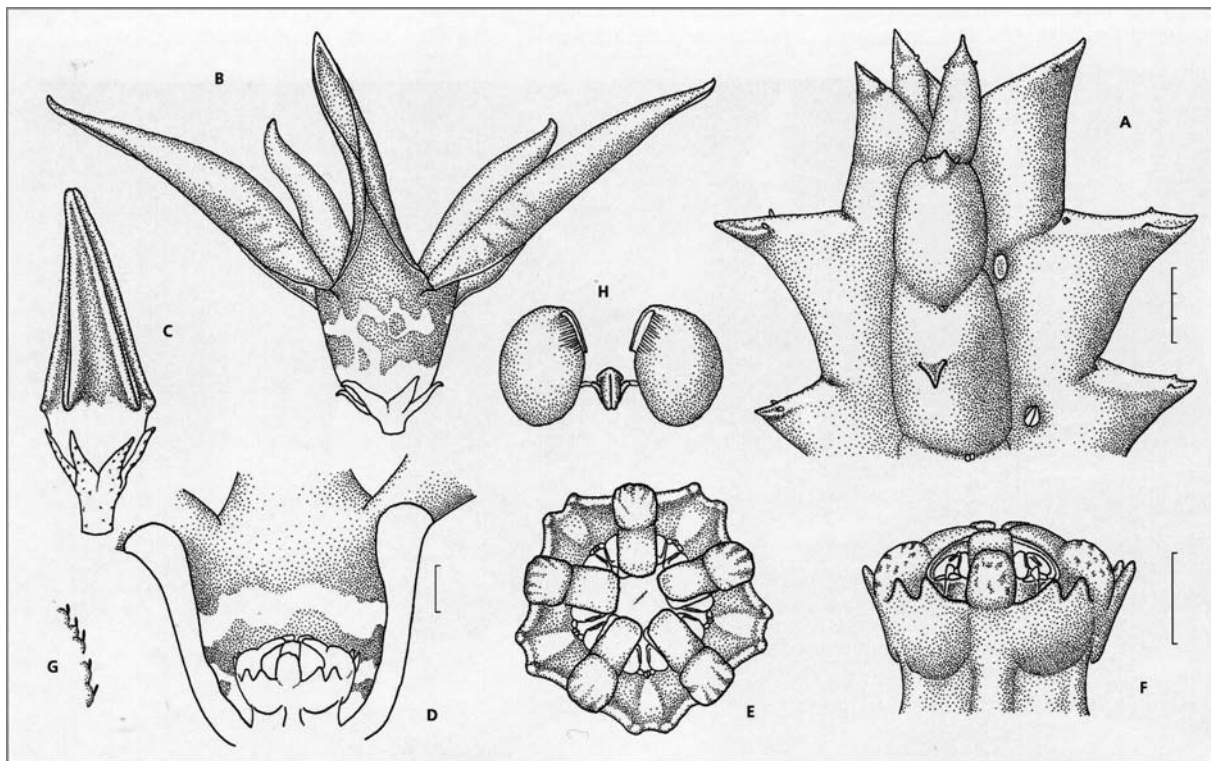


Fig. 13.106. *Quaqua arenicola* subsp. *arenicola*. A, apex of stem. B, side view of flower. C, bud. D, side view of dissected flower. E, face view of gynostegium. F, side view of gynostegium. G, papillae inside corolla in mouth of tube. H, pollinarium. Scale bars: A-C, 3 mm (at A); D, 1 mm; E, F, 1 mm (at F); G, 0.5 mm (at A); H, 0.25 mm (at A). Drawn from: C. Bayer 1978, south-east of Touwsriver; rest, Williams 128, south-east of Sutherland.

15a. *Quaqua arenicola* subsp. *arenicola*

Inflorescence with flowers mostly opening in lower half of stem. **Corolla** 20-30 mm diam.; inside velvety, dark maroon to purple-black on lobes and into mouth of tube, below this banded with same dark colour on cream, with low rounded papillae each tipped with a short bristle around mouth of tube only; **tube** $\pm$ 4-5 mm long, 4-5 mm broad at mouth, cupular; **lobes** 10.5-15.0 mm long, 3.5-4.0 mm broad at base, margins strongly folded back except at base (so ovate near base then slender above). **Corona** 2.5-3.0 mm diam., yellow to pale red, raised on stipe up to 0.5 mm long; **outer lobes** erect, with darker reddish tips; **inner lobes** with broad swollen dorsal projection often flecked with purple-red.

Distribution and habitat

Subsp. *arenicola* has a scattered and wide distribution around the southern and western edges of the Great Karoo. Records have been made from within the winter-rainfall area near the Hex River Pass. This appears to be its western limit and from here it extends to Touws River, eastwards to Matjiesfontein and further east to round Prince Albert and near Willowmore. I was also shown some plants on a farm a little west of Rietbron in the Great Karoo, so it might well be more widely distributed in the southern portion of the Great Karoo. There are also some



Fig. 13.107. *Q. arenicola* subsp. *arenicola*, PVB 7808, north-west of Montagu.

records from the eastern part of the Little Karoo near Uniondale and a single record from the Klein Roggeveld south-east of Sutherland.

N.S. Pillans first found plants growing in soft sand, from where it obtained its name, but generally it grows on stony ground in low-lying areas or gentle slopes in the shelter of small shrubs.

Diagnostic features and relationships

Plants of subsp. *arenicola* form dense but low clumps up to 500 mm in diameter. The stems are robust and thick but relatively short. Along the stems the tubercles make up four strong, regular angles with the sides flat or slightly concave between them. Each tubercle is tipped

with a stout tooth which is initially quite sharp but later wears down to a blunt, grey knob. It is subtended by one or more stipular denticles.

Flowers of subsp. *arenicola* are produced in dense clusters towards the bases of the stems. They are amongst the largest in the genus and may reach 30 mm across. Despite their unpleasant smell they are quite attractive, especially when they open fully. Inside, the corolla is deep maroon to purple-black on the lobes and into the mouth of the tube. Below this there are one or two rings and bars of this dark colour on a cream background. The dark parts are made particularly attractive by their finely velvety texture. Papillae are present on the inside, but they are restricted to the mouth of the tube.

In subsp. *arenicola* the corona is usually yellow, with a few dark patches towards the tips of the outer lobes and beneath the guide-rails. It consists of the usual cupular outer series and small, roughly rectangular inner lobes, each of which has a swollen, rounded dorsal projection.

History

Quaqua arenicola subsp. *arenicola* was discovered near Matjiesfontein by N.S. Pillans in 1900 and was also gathered in the same area by Harold H.W. Pearson in 1914.



Fig. 13.108. *Q. arenicola* subsp. *arenicola*, PVB 6181, Matjiesfontein, April 1995.

QUAQUA ARENICOLA

15b. *Quaqua arenicola* subsp. *pilifera*

Quaqua arenicola subsp. *pilifera* (Bruyns)

Bruyns, Bot. Jahrb. Syst. 121: 383 (1999).

Q. armata subsp. *pilifera* Bruyns, Bradleya 1: 68 (1983).

Quaqua pilifera (Bruyns) Plowes, *Excelsa* 16: 98 (1994).

Type: Cape, south-east of Middelpos, Dec. 1974, Bayer & Bruyns 826 (NBG).

Inflorescence with flowers opening at any height on stem, often towards base. **Corolla** 15-25 mm diam.; inside dull dark purple-brown on lobes and into mouth of tube, below this speckled with same on cream, covered with conical obtuse papillae (reaching max. length at base of lobes) each tipped with a bristle; **tube** 2-3 mm long, 3-4 mm broad at mouth, broadly cupular; **lobes** 7.5-10.0 mm long, 4 mm broad at base, margins folded back for most of length but not tightly so lobe narrows gradually from base to acute apex. **Corona** 2.0-2.2 mm diam., reddish purple, raised on very short stipe; **outer lobes** erect to slightly spreading; **inner lobes** with small slightly swollen dorsal projection.

Distribution and habitat

Subsp. *pilifera* is found only on the Roggeveld plateau and is now known from several farms a little south of Middelpos and in various places west and south of Fraserburg.

Plants grow on stony slopes usually consisting of bluish shale with dolerite rocks scattered around. A few have been found on dolerite dykes. Specimens usually shelter around the base of a bush or, occasionally, alongside a rock.

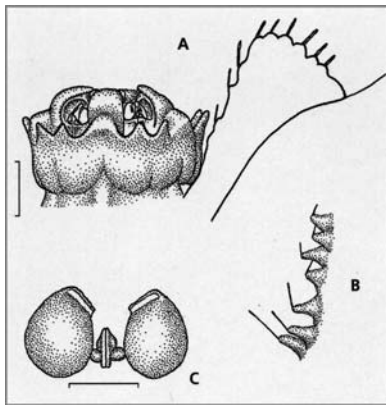


Fig. 13.111. *Quaqua arenicola* subsp. *pilifera*. A, side view of gynostegium. B, papillae inside corolla from base of lobes. C, pollinarium. Scale bars: A, 0.5 mm; B, 0.5 mm (at C); C, 0.25 mm. Drawn from PVB 4015, south of Middelpos.



Fig. 13.109. *Q. arenicola* subsp. *pilifera*, PVB 5983, south-west of Fraserburg.



Fig. 13.110. *Q. arenicola* subsp. *pilifera*, PVB 4015, south of Middelpos.

Diagnostic features and relationships

In subsp. *pilifera* the stems are produced in dense, tightly packed clumps up to 500 mm in diameter and cannot be distinguished at all from those of subsp. *arenicola*.

Flowers of subsp. *pilifera* are smaller than those of subsp. *arenicola* (though just as evil-smelling) and have papillae all over the inside. This gives them a rough and dull appearance which is quite unlike the rich, velvety sheen on the corolla of subsp. *arenicola* where these larger papillae are only present in the mouth of the tube. The papillae themselves reach a slightly greater length and their apical bristles are usually longer than will be seen in subsp.

arenicola. Other small and rather less reliable differences are found in the corona. This is a little smaller and darker than in subsp. *arenicola* and the inner lobes have a smaller dorsal projection.

History

As far as can be ascertained, the first record of this subspecies was made by M. Bruce Bayer and the present author in December 1974 during a field trip to investigate *Pectinaria longipes* and *P. articulata* to the north of Sutherland. The existence of this taxon in the area between Sutherland and Fraserburg seems to have been established first by A.S. Theron, who found it on his own farm.

16. *Quaqua mammillaris*

Quaqua mammillaris (L.) Bruyns, *Bradleya* 1: 63 (1983).

Stapelia mammillaris L., *Mant. Pl.* 2: 216 (1771).

Pectinaria mammillaris (L.) Sweet, *Hort. Brit.*, ed. 2: 357 (1830).

Piaranthus mammillaris (L.) G.Don, *Gen. Hist.* 4:114 (1837-8).

Boucerosia mammillaris (L.) N.E.Br., *J. Linn. Soc. Bot.* 17:165(1878).

Caralluma mammillaris (L.) N.E.Br., *Hooker's Icon. Pl.* 20: sub t.1902 (1890).

Lectotype: South Africa, Cape, Burman, *Rar. afric. pl.*: t.11 (1738-9).

Stapelia pulla Aiton, *Hort. Kew.*, ed. 1, 1: 310 (1789).

Piaranthus pullus (Aiton) Haw. *Syn. Pl. Succ.*: 44 (1812).

Type: South Africa, Cape, Karoo, Masson (BM).

Sarcophagophilus winklerianus Dinter, *Feddes Repert Spec. Nov. Regni Veg.* 19:156 (1923), as *S. winkleri*.

Caralluma winkleriana (Dinter) A.C.White & B.Sloane, *Step.*, ed. 2, 1: 277 (1937), as *C. winkleri*.

Type: Namibia, Klinghardt Mountains, 1922, *Dinter* 472 (PRE, holo.; WIND, iso.).

Sarcophagophilus armatus Dinter, *Feddes Repert. Spec. Nov. Regni Veg. Beih.* 53:107 (1928) non (N.E.Br.) Dinter (1928).

Lectotype: Namibia, Vahldorn, *Dinter* 5112 (PRE).

Often robust succulent shrub up to 600 mm diam., rooting from single central stem only. **Stems** 120-500 mm long, 15-10 mm thick, erect, uniformly green to purple or brown, occasionally mottled with purple-brown or green; **tubercles** 5-20 mm long, conical to slightly laterally flattened, spreading, fused near base into 4-5 irregularly arranged angles, each tipped with sharp hardened yellow-brown tooth. **Inflorescences** of 3-15 ± simultaneously opening flowers usually in dense fascicles mostly in upper two thirds of stem; **pedicel** 2-3 mm long, 2 mm thick, spreading and holding flower facing horizontally; **sepals** 3-4 mm long, ovate, acuminate. **Corolla** 20-27 mm diam., campanulate to nearly rotate; outside pale-green towards base, otherwise purple-brown; inside purple-black to red on lobes and into mouth of tube where breaking up and becoming spots and bands on cream to white in tube, with low to conical obtuse papillae mainly on lower half of lobes and mouth of tube, each topped with a thick ascending bristle; **tube** 3-5 mm long, ± 5 mm broad at mouth, cupular, corolla thickened at mouth; **lobes** 10-20 mm long, 4.5-7.0 mm broad at often ovate base, erect to spreading, narrowly lanceolate, usually tapering from base to finely acute often slightly incurved apex, strongly longitudinally folded back down middle. **Corona** ± 3 mm tall, 4.0-4.5 mm broad, dark purple-brown, raised on short stipe; **outer lobes** 1.5-2.0 mm long, erect, bifid to nearly halfway down into erect deltoid teeth (sometimes with small denticle between them) laterally fused for most of length with bases of inner lobes to form deep pouch; **inner lobes** ± 1 mm long, adpressed to backs of anthers and exceeding them, then connivent-erect and rising into small column in centre, linear, obtuse, dorsiventrally flattened, with erect truncate to obtuse dorsal projection slightly in front of outer lobes.

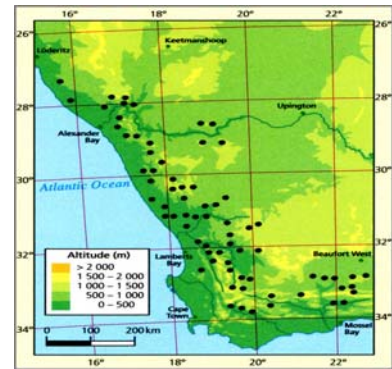


Fig. 13.112. Distribution of *Quaqua mammillaris*.

Distribution and habitat

Quaqua mammillaris is the most widely distributed of all species of *Quaqua* and occurs over most of the western parts of the Karoo. It is found from the Klinghardt Mountains south of Lüderitz in Namibia southwards into Namaqualand and right across the drier parts of the Northern and Western Cape, mainly west of the escarpment, to as far east as near Rietbron in the Great Karoo and Oudtshoorn in the Little Karoo. It also occurs in the area around Warm-

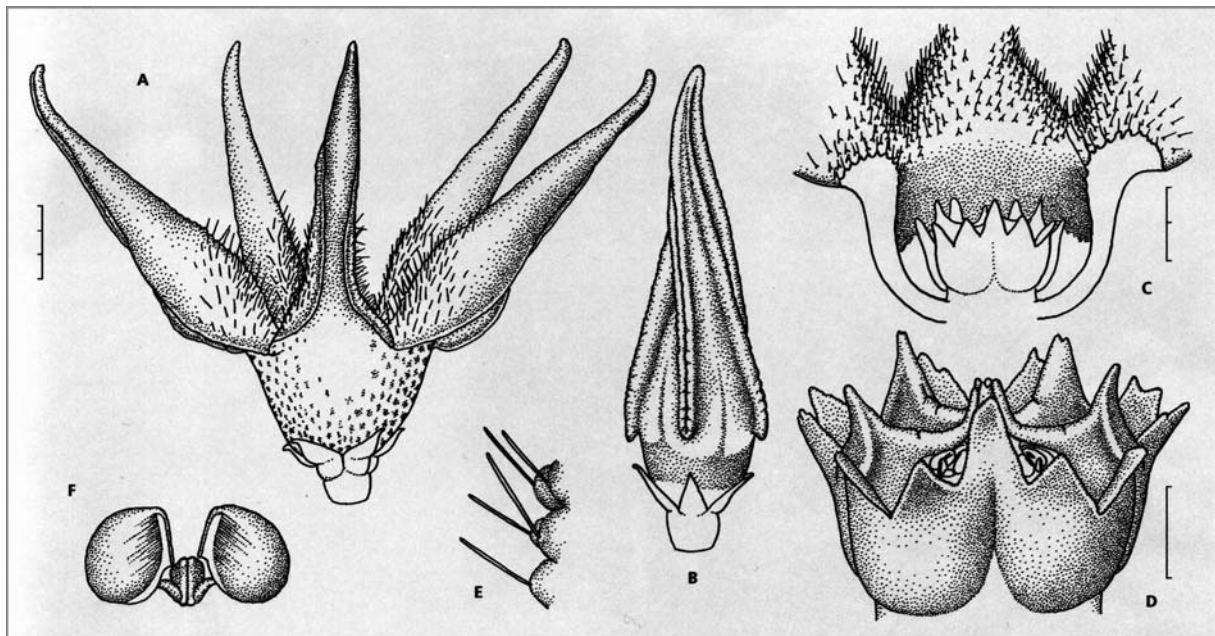


Fig. 13.113. *Quaqua mammillaris*. A, side view of flower. B, bud. C, side view of centre of dissected flower. D, side view of gynostegium. E, papillae inside corolla in mouth of tube. F, pollinarium. Scale bars: A, B, 3 mm (at A); C, 2 mm; D, 1 mm; E, 0.5 mm (at A); F, 0.25 mm (at A). Drawn from: B, PVB 2616, between Bloutoring and Hoek van die Berg, Little Karoo; rest, PVB, Botterkloof.

QUAQUA MAMMILLARIS

bad in Namibia and Pofadder in Bushmanland of South Africa.

Over so large an area, it is natural that this species grows in a wide variety of habitats. Thus it is found from the red sand of the coastal *sandveld* of Namaqualand to stony slopes on hills and mountains and in quartz patches around Pofadder. Smaller plants are generally found growing inside or near another shrub but larger specimens may be seen growing in the open where they assume a shrubby habit rather like that in species such as *Hoodia gordonii*.

Diagnostic features and relationships

Plants of *Q. mammillaris* form robust, densely branched shrubs and may be up to 600 mm tall and broad. Generally *Q. mammillaris* is easily recognised by its usually uniformly coloured, erect stems, which branch mostly from their base and root from the central stem only. It is noteworthy that in this species, unlike several others that also only root centrally, cuttings are very difficult to root. The tubercles on the stems are irregularly arranged and rarely form the four neat rows found in most of the other species. They are also very sharply armed with a hard, yellow-brown spike and these make the plants thorny and difficult to handle.

The flowers, which reach 27 mm across, are among the largest in the genus. They are

produced in large numbers in many dense, more or less simultaneously opening clusters and emit a strong, foul smell so that a plant in flower can often be detected from some distance away before it is seen. The lobes taper progressively from the base to a fine point and are strongly folded along the middle, which makes them quite slender. Usually they do not spread out much but this is mainly because of overcrowding in the inflorescences. On the inside they are dark purple-black and this dark colour continues just into the mouth of the tube, where it breaks up to form spots and rings on a white background in the tube. This tube is comparatively deep and it is slightly constricted at the mouth by thickening there of the corolla. Most of the inside of the flower is covered with papillae tipped with bristles which reach their greatest length in the mouth of the tube but disappear lower down.

The dark corona consists of a cupular outer series and inner lobes which, after covering the anthers, rise in a small column in the centre. They have an erect dorsal projection more or less in series with the lobules of the outer corona.

Although vegetatively and florally relatively uniform over most of its range, there are two ecological races which differ in some respects. One of these is what Dinter baptised *Sarcophagophilus winklerianus*. In Namibia this is known in the Klinghardt Mountains and in the

Schakalsberge as well as further east between Lorelei and the mouth of the Fish River. It is also known further south near Annisfontein in the western Richtersveld of South Africa. Plants usually grow on rocky, schist or dolomitic slopes among many other succulent shrubs. The broader stems with more scattered, larger and very triangular tubercles lend it a generally heavier appearance than the typical form but florally it cannot be distinguished from typical *Q. mammillaris*.

In the other race, the stems are narrower (usually only 15–20 mm thick), they are conspicuously mottled with purple-brown on paler green and often have quite thin, long teeth on the tubercles. Plants may occasionally root on side-branches, a phenomenon otherwise never seen in *Q. mammillaris*, and, perhaps as a consequence, they may form quite low, spreading and very dense clusters. The flowers are, however, the same as those of typical *Q. mammillaris*. This is an ecotype which is restricted to soils derived from sandstones. It is found around Citrusdal, in a few scattered, dry localities in the Cedarberg and Swarttruggens south-eastwards to near Karooport and also in a few spots in sandstones east and south-east of Touws River. Plants usually grow in semi-arid, transitional *fynbos* among scattered specimens of the succulent Aizoaceae, *Pelargonium alternans* and various species of *Crassula*, often with clumps of *Protea* and *Restionaceae*



Fig. 13.114. *Q. mammillaris*, PVB 9891, on quartz outcrop near Naroegas, a medium-sized specimen about 0.4 m broad, June 2004.



Fig. 13.115. *Q. mammillaris*, PVB 9891, near Naroegas, June 2004.



Fig. 13.116. *Q. mammillaris*, PVB 6384a, near Avondrust, the form with slender, mottled stems, from sandstone substrate.

in evidence. They often occur on horizontal or gently sloping sandstone slabs where the soils are especially shallow.

History

As *Q. mammillaris* is both widespread and generally fairly common, it is probably the best known of all species of *Quaqua* and was among the first four stapeliads to become known to science. It would appear that it was first noticed by Paul Hermann, a German by birth who studied medicine in Holland and was later employed by the Vereenigde Oost-indische Company. Hermann visited the Cape in 1672 on his way to Ceylon and made a collection of herbarium specimens there. At the time of his death in 1695 he was busy writing an inventory of the plants that he had collected at the Cape and this was published by Johannes Burman, professor of Botany at Amsterdam as an appendix to his *Thesaurus Zeylanicus* (Burman 1737). In it there is the first probable mention of *Q. mammillaris*. The first figure of it was published in the following year by Burman (1738-9). For some reason Linnaeus took no notice of this until well after 1753 and he gave it a binomial only in 1771. Masson was, of course, well aware of this species but he called it *Stapelia pulla*, in reference to its very dark flowers.

17. Quaqua pillansii

Quaqua pillansii (N.E.Br.) Bruyns, *Bradleya* 1: 69 (1983).

Caralluma pillansii N.E.Br., *Fl. Cap.* 4 (1): 876 (1909).

Type: South Africa, Cape, near Montagu, N.S.

Pillans 678 (K, holo.; BOL, iso.).

Robust succulent shrub up to 0.5 m tall and 0.6 m broad, rooting from a single central stem only. **Stems** 150-400 mm long, 20-40 mm thick, erect, grey-green mottled with purple-brown; **tubercles** 8-15 mm long, deltoid, laterally flattened, spreading, joined in lower half into 4 thick obtuse angles along stem, each tipped with a blunt to sharp hardened yellow to brown tooth. **Inflorescences** of 4-20 ± simultaneously opening flowers usually in dense fascicles mostly in upper half of stem; **pedicels** 1-2 mm long, 2 mm thick, often thickening towards calyx, spreading and holding flower facing horizontally; **sepals** 2-3 mm long, ovate-acute, speckled with purple. **Corolla** 12-18 mm long, 8-17 mm diam., campanulate; outside somewhat shiny, dark purple-brown to pale red lightening to cream speckled with purple-red towards base; inside spotted and transversely mottled with dark to pale purple-brown or maroon on cream, covered except in base of tube around corona with low obtuse papillae each tipped with an ascending purplish bristle up to 1 mm long (longest in mouth of tube); **tube** 4.5-6.0 mm long, 3-4 mm broad at mouth, ± elliptical, with corolla much thickened around mouth; **lobes** 7-11 mm long, 4-6 mm broad, erect to spreading, oblong-ovate, very shortly acute, lightly folded back longitudinally so that ventral surface convex. **Corona** 2.0-2.5 mm tall, 2-3 mm broad, raised on short stipe; **outer lobes** 0.8-1.2 mm long, ascending-erect, ± truncate-emarginate, laterally fused for whole length with bases of inner lobes to form deep pouch, dark purple-brown; **inner lobes** ± 1 mm long, usually sloping upwards at about 45° to horizontal, adpressed to backs of others in lower half and exceeding them to touch in centre, rectangular to broadly deltoid, broadly obtuse and sometimes emarginate, dorsiventrally flattened, with broadly swollen obtuse to truncate-emarginate dorsal projection in series with outer lobes, margins and dorsal projection purple-brown, otherwise yellow suffused with red to dark purple.



Fig. 13.117. *Q. pillansii*, PVB 7049, steep slopes on the side of a ravine near Cockscomb Peak south of Steytlerville with *Adromischus sphenophyllus*, January 1997.

Distribution and habitat

Quaqua pillansii has been found to be widely distributed from the south-western to the Eastern Cape. It occurs from just south of Ceres in the south-western Cape through most of the Cape fold mountains (except the Outeniqua and Langeberg) to the western edge of the Suurburg, north of Kirkwood.

This species always grows on soils derived from sandstones. Plants are usually encountered on hot and dry, stony, north-facing slopes or on the dry sides of ravines. Such places are populated by a mixture of karroid and *fynbos* elements: among the trees and shrubs are such species as *Heeria argentea*, *Dodonea viscosa*, species of *Rhus*, *Passerina* and *Restio gaudichaudianus*, but in these often locally semi-arid spots there is a distinct bias towards succulents with various species of succulent Aizoaceae, many species of *Crassula* (often *C. arborescens*, *C. rupestris* and *C. multiflora*) and frequently *Aloe mitriformis*/*A. comptonii*.

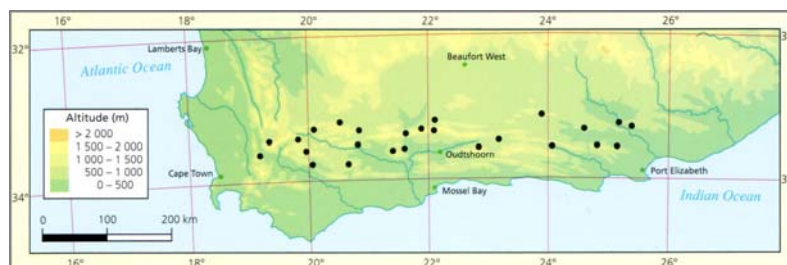


Fig. 13.118. Distribution of *Quaqua pillansii*.

QUAQUA PILLANSII



Fig. 13.119. *Q. pillansii*, PVB 1438, near Mitchell's Pass, Ceres.



Fig. 13.120. *Q. pillansii*, PVB 1438, near Mitchell's Pass, Ceres.



Fig. 13.121. *Q. pillansii*, Kogman's Kloof, Montagu.

Diagnostic features and relationships

Quaqua pillansii is probably the most handsome and striking member of a genus where the plants are generally rather dull-looking. The robust stems are up to 300 mm long and form a substantial shrub (fig. 13, 13.117) sometimes nearly half a meter in height and even more in diameter, which roots only on the main central stem (though cuttings are readily rooted). The imposing size of these plants is only exceeded occasionally in *Q. mammillaris*. The stems are beautifully mottled with purple-brown on a grey-green background. They have large, deltoid, laterally flattened tubercles which are joined into four broad wings along the stems. Each tubercle is tipped with a blunt but hard tooth. Nevertheless, despite the size of the plants, they are not always particularly easy to find. Plants are, for one thing, often very few and far between but, in addition, the jagged teeth and mottling of the stems break up their outlines to provide an effective camouflage

which enables them to blend in remarkably with their surroundings of sandstone rocks and bushes.

The flowers are also unmistakable. They are produced in dense, more or less simultaneously-opening clusters and they emit a strong, somewhat fruity, unpleasant odour. Outside, the corolla is dark and often somewhat shiny but inside it is covered by a very rich combination of cream mottled with roundish spots and transverse markings of purple-brown or maroon. The lobes are broad and ovate and usually spread out only slightly so that the flower is distinctly campanulate. In the centre there is a small but relatively deep, cupular tube whose mouth is slightly constricted by the thickened tissue of the corolla. The interior is covered with papillae, in some plants densely and extensively, but in others these are found only around the mouth of the tube. Each papilla has an elongated apical bristle and these bristles are longest in the tube and around its mouth.

The corona is seated on a short stipe right

in the base of the tube. It has short, blunt outer lobes united into a cup around the anthers and inner lobes which are broad and usually rise somewhat in the centre, rather above the level of the anthers. The whole structure varies from nearly entirely dark purple to dark on the outer lobes and paler yellow on the inner.

History

Quaqua pillansii was discovered by N.S. Pillans in the mountains just west of Montagu in October 1904. It was always rather little known, so White & Sloane (1937) could not find an illustration for it and seem not to have seen any living material of it at all. However, Lückhoff (1952) did manage to photograph it and today it is known over a wide area in drier spots among the fold mountains of the Cape.

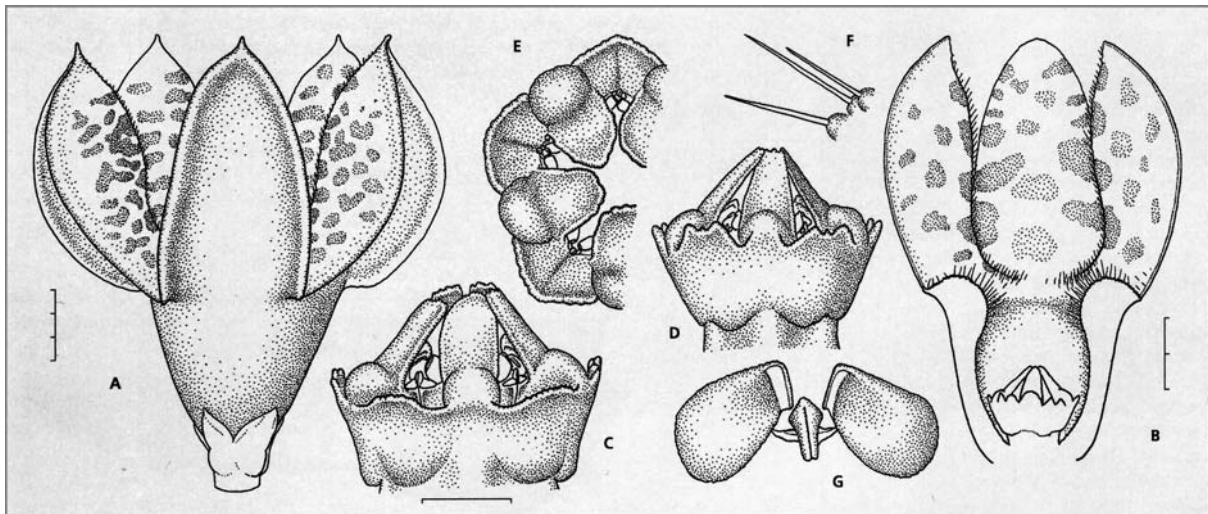


Fig. 13.122. *Quaqua pillansii*. A, side view of flower. B, side view of dissected flower. C, D, side view of gynostegium. E, part of face view of gynostegium. F, papillae inside corolla from around mouth of tube. G, pollinarium. Scale bars: A, 3 mm; B, 2 mm; C-E, 1 mm (at C); F, 0.5 mm (at A); G, 0.25 mm (at A). Drawn from: A, C, E, G, PVB 2229, south-west of Calitzdorp; B, D, F, PVB 1438, near Mitchell's Pass, Ceres.

18. *Quaqua linearis*

Quaqua linearis (N.E.Br.) Bruyns, *Bradleya* 1: 71 (1983).

Caralluma linearis N.E.Br., *Hooker's Icon. PL* 20: t. 1903 A (1890).

Type: South Africa, Cape, Seven Weeks Poort, *Bain* 8 (K).

Small succulent up to 200 mm tall and 150 mm broad, rooting on central stem only and branching mainly above base. **Stems** 50-200 mm long, 10-25 mm thick, erect, uniformly dark green to purple-black and particularly dark on young growth; **tubercles** 2-5 mm long, broadly deltoid, laterally flattened, spreading, joined into 4 obtuse angles along stem, each tipped with small hardened deltoid tooth mostly < 1 mm long flanked by 2 very small stipular denticles. **Inflorescence** of 1-6 often simultaneously opening flowers in lax fascicles mainly in upper parts of stem; **pedicel** 1-7 (-10) mm long, 1.5 mm thick, spreading and holding flower facing horizontally; **sepals** 2.0-2.5 mm long, ovate-acute. **Corolla** 12-18 mm long, 9-22 mm diam., usually campanulate; outside red-purple on lobes becoming white towards base of lobes and on tube; inside white in tube and on base of lobes and dark red-purple above, glabrous and smooth; **tube** 3-1 mm long, 5 mm broad at mouth, cupular, with corolla

scarcely thickened at mouth; **lobes** 8-14 mm long, 2-4 mm broad at base, erect to spreading, strongly folded back longitudinally along middle so that most of lobe only 1 mm broad, often widening again slightly before abruptly acute and slightly incurved apex. **Corona** $\pm$ 2.5 mm tall, 2.2-2.8 mm broad, purple on lobes becoming white towards base, raised on very short stipe; **outer lobes** $\pm$ 1 mm long, erect, shortly bifid into $\pm$ erect deltoid obtuse lobules (sometimes with denticle between them), fused laterally in lower half to bases of inner lobes to form deep pouch; **inner lobes** 2 mm long, adpressed to backs of anthers then rising in column above centre and curving outwards, linear, obtuse, dorsiventrally flattened, without dorsal projection.



Fig. 13.123. *Q. linearis*, PVB 7524, northern slopes of Warmwaterberg.

Distribution and habitat

At present *Q. linearis* is known in the mountainous terrain which forms the north-western boundary of the Little Karoo, from south of Laingsburg westwards to near Touws River. Most of this terrain forms part of the Witberge or lies between the Witberge and the Anysberg. The species is also known on the Warmwaterberg, which lies considerably further south in the Little Karoo.

Like *Q. pillansii*, *Q. linearis* is exclusively a plant of soils derived from sandstones but in this case it is mainly confined to those of the Witteberg series where it grows on stony slopes and flat rocky areas among shrubs. It is often associated with an odd and characteristic assemblage of species which may be encountered on many of the slopes and higher, flatter hilltops in this area. This association includes *Pteronia fastigiata*, a small-leaved, compact-growing and rather bright pink form of *Crassula rupestris* and *Braunsia apiculata*, among many others.

Diagnostic features and relationships

In *Q. linearis* the plant forms a small and usually compact shrub. This mostly does not exceed 150 mm in height and diameter and roots by the central stem only, though cuttings are readily rooted. The young stems are exceptionally dark in colour and may be practically black. Although the tubercles are a little more prominent than in *Q. ramosa*, they are rounded and still quite obscure, and are joined into obtuse angles along the stem. Unlike in *Q. ramosa*, in *Q. linearis* each tubercle bears a quite obvious, albeit minute tooth, which is flanked by two even tinier stipular denticles (fig. 19 H).

The flowers arise on small inflorescences towards the tips of the stems and are produced in unusually modest numbers for this section: they are frequently solitary or in lax groups of only two or three. The corolla lobes are tightly folded for most of their length so they are slender, only widening suddenly at the base. For most of their length they are a dark red-purple and this changes suddenly on the widened

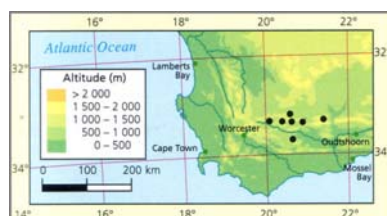


Fig. 13.124. Distribution of *Quaqua linearis*.

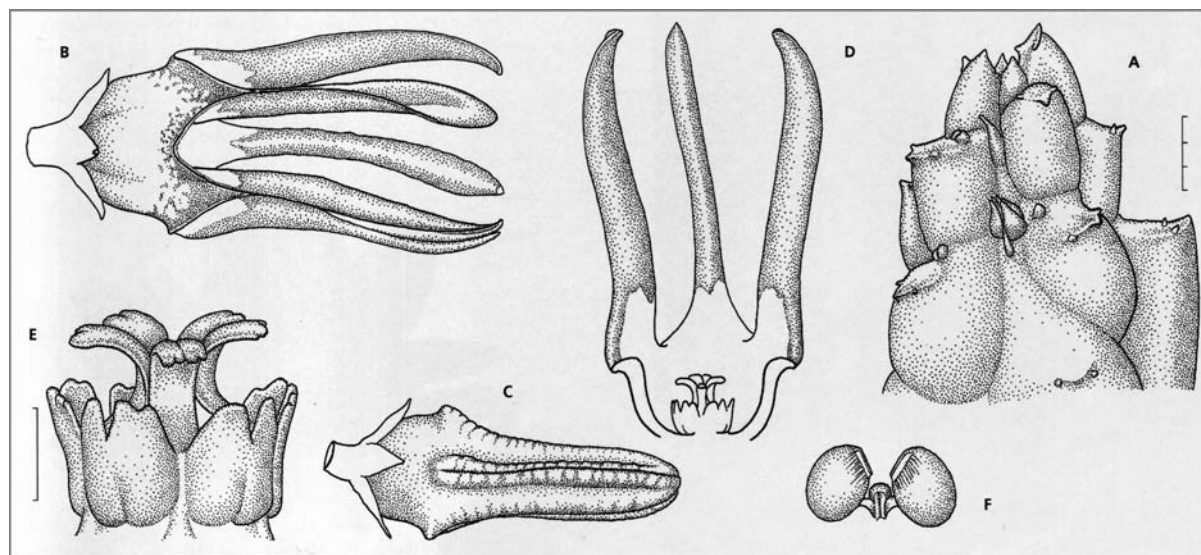


Fig. 13.125. *Quaqua linearis*. A, apex of stem. B, side view of flower. C, bud. D, side view of dissected flower. E, side view of gynostegium. F, pollinarium. Scale bars: A-D, 3 mm (at A); E, 1 mm; F, 0.25 mm (at A). Drawn from PVB 2822, Avondrust.

QUAQUA RAMOSA

basal part to white. This white colour continues into the short, but quite deeply cup-shaped tube. The entire corolla is made of a relatively thin fabric which is devoid of bristles or papillae inside. The flowers emit a faint, unpleasant, excrement-like odour.

In the base of the tube, well separated from its sides, is the gynostegium. The outer corona lobes are fused together into a deep cup while the inner lobes are more unusual: initially adpressed to the anthers, they rise in the centre in a short column and then spread out. This arrangement is unique in the genus.

History

Quaqua linearis was originally discovered by Thomas C. Bain in Seweweekspoort in the Little Swartberg in 1875. The next recorded collection was made by Joseph Archer on the lower slopes of the Witberge near Whitehill in 1934, and then it languished once more in obscurity, known in the flesh neither to White & Sloane nor to Carl Lückhoff. Eventually it was re-collected in January 1976 (Bruyns 1977), also in the Witberge.



Fig. 13.126. *Q. linearis*, PVB 6180, south-west of Laingsburg.



Fig. 13.127. *Q. linearis*, PVB 6180, south-west of Laingsburg, in habitat, October 1994, with small form of *Crassula rupestris* subsp. *rupestris*.

19. Quaqua ramosa

Quaqua ramosa (Masson) Bruyns, *Bradleya* 1: 74 (1983).

Stapelia ramosa Masson, *Stap. Nov.*: 21, t. 32 (1797).

Piранthus ramosus (Masson) Sweet, *Hort. Brit.*, ed.

2: 359 (1830).

Caralluma ramosa (Masson) N.E.Br., *Hooker's Icon.*

PL 20: t. 1904 (1890).

Type: South Africa, Cape, near Warmwaterberg, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 32.

Densely branched succulent shrublet usually broader than tall, up to 0.3 m tall and 0.3 m broad, rooting from central stem only and branching mainly above base. **Stems** 60-300 mm long, 15-30 mm thick, erect, purplish or greyish green; **tubercles** 3-5 mm long, broadly deltoid, laterally flattened, obtuse, joined in lower half into 4 (rarely 5) obtuse angles along stem, each tipped with very small tooth < 0.5 mm long or corky brownish patch flanked by 2 obtuse stipular denticles on new growth. **Inflorescences** of 2-15 ± simultaneously opening flowers usually in dense fascicles mostly in upper half of stem; **pedicel** 1.5-3.0 mm long, 1.5 mm thick, pinkish, spreading and holding flower facing horizontally; **sepals** 2-3 mm long, lanceolate-acute, pinkish. **Corolla** 13-15 mm long, narrowly campanulate; outside smooth and somewhat shiny purple-black on lobes to red on tube becoming cream towards base; inside dark purple-black on lobes and mouth of tube, in tube white with large round purple-black spots, with papillae around mouth of tube each tipped with a white ascending bristle; **tube** 3-4 mm long, 2.5-5.0 mm broad at mouth, cupular, with corolla slightly thickened at mouth; **lobes** 7.5-12.0 mm long, 3.5-4.0 mm broad at base, erect to spreading, narrowly lanceolate, acute, longitudinally folded back along middle. **Corona** ±1.5 mm tall, 2.0-2.2 mm broad, purple-black becoming white towards base, raised on short stipe; **outer lobes** ± 0.5 mm long, ascending, shortly bifid into small spreading deltoid teeth, fused laterally for most of length with bases of inner lobes to form pouch; **inner lobes** ± 0.5 mm long, adpressed to backs of anthers and exceeding them to meet in centre, ± rectangular, obtuse, dorsiventrally flattened, with broad and obtuse dorsal projection near base.



Fig. 13.128. *Q. ramosa*, PVB, Lemoenhoek, north-east of Barrydale.

QUAQUA RAMOSA

Distribution and habitat

Quaqua ramosa is of regular, though rarely very common occurrence in the Little Karoo from Montagu eastwards to near Oudtshoorn. It also occurs, though somewhat more sporadically, in the Great Karoo from around Laingsburg northwards and eastwards, but it does not appear to extend as far as either Leeu Gamka or Prince Albert.

Plants are found on various kinds of shales, tillites and alluvial deposits and seem to avoid sandstones. They usually grow on stony slopes or hilltops, mostly inside or alongside other bushes and with a wide selection of other succulents.

Diagnostic features and relationships

Specimens of *Q. ramosa* form shrubs rooted by a central stem and may reach 300 mm tall and broad. In this species branches will root in cultivation, but this happens slowly and with difficulty. Plants are usually densely branched somewhat above the base. The stems of *Q. ramosa* are most unusual and their unmistakable shape was very accurately portrayed by Masson, who figured this species for the first time in his book *Stapeliae Novae*. The four thick and rounded continuous angles are made up of obscure, rounded and rather 'mammose' tubercles which are practically devoid of an apical tooth (shown here in an SEM picture in fig. 17 E). Young stems are greenish but soon they become grey and most of the plant has this grey colour, looking rather like pieces of old wood. It is from this that the popular name *ou ram* or 'old goat' is derived.

In *Q. ramosa* the flowers are produced towards the apices of the stems on quite conspicuous peduncular patches and they usually open together in dense clusters. They have a strong and unpleasant smell of sheep or buck urine. The corolla lobes are strongly folded down the middle but rarely spread out very far, mainly because of congestion in the inflorescence. They are dark purple-black both inside and outside, with the outside fairly shiny. On the inside they are not at all shiny, becoming densely papillate towards their bases and in the mouth of the tube. The tube, which is cup-shaped and about twice as deep as the height of the gynostegium, is white with dark spots and is slightly thickened around the mouth.

In *Q. ramosa* the gynostegium is broader than tall, with very small outer lobes along the sides and with the inner lobes just covering the anthers.

Quaqua ramosa is clearly closely related to *Q. mammillaris* and *Q. arenicola* and all these species have flowers which are hard to distinguish between. They are most easily separated vegetatively, with the unusual stems of *Q. ramosa* making it unmistakable.

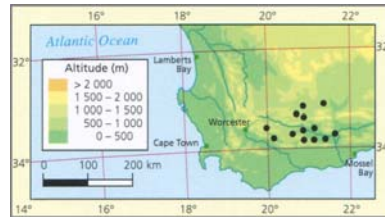


Fig. 13.129. Distribution of *Quaqua ramosa*.

History

Quaqua ramosa was discovered by Francis Masson and flowered in August 1792 in his garden at Cape Town. He found his plants in the Little Karoo near the hot springs beyond 'Plattekloof'. The map reproduced by Burchell (1822-4) shows that the 'Plattekloof' referred to by Masson corresponds to the present-day Gysmanshoek Pass and so these 'hot springs' are likely to correspond to those at the Warmwaterberg. It seems therefore that Masson found this species somewhere near the eastern corner of the Warmwaterberg, where it is not uncommon even today.



Fig. 13.130. *Q. ramosa*, PVB 7339, Plathuis, Little Karoo, a medium-sized plant bearing many, still immature follicles, in habitat, September 1997.

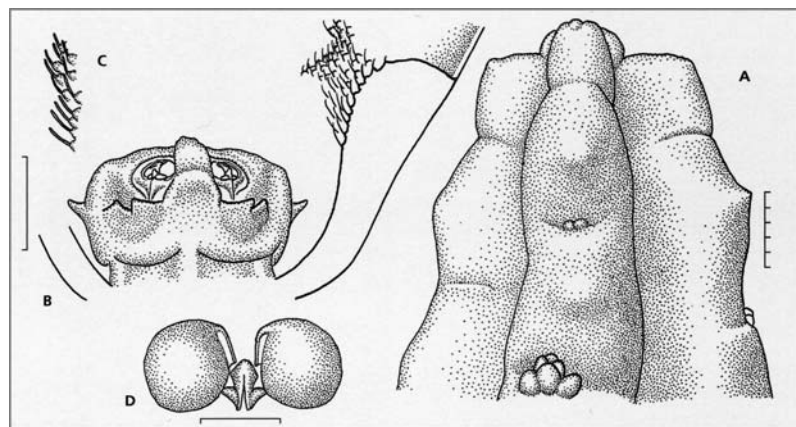
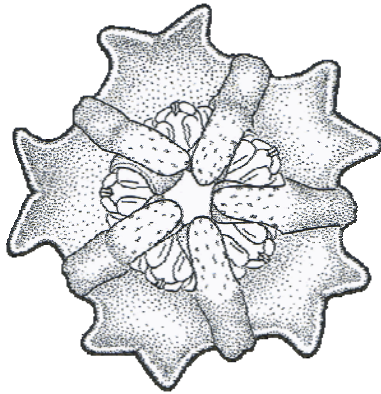


Fig. 13.131. *Quaqua ramosa*. A, apex of stem. B, side view of gynostegium. C, papillae inside corolla in mouth of tube. D, pollinarium. Scale bars: A, 5 mm; B, 1 mm; C, 0.5 mm (at D); D, 0.25 mm. Drawn from PVB, Lemoenshoek, north-east of Barrydale.

14. Richtersveldia



The single species of *Richtersveldia* was transferred from *Notechidnopsis* by Meve & Liede (2002). Some evidence suggests that this species is more closely related to genera such as *Duvalia*, *Huernia*, *Laryleachia* and *Orbea* than it is to *Notechidnopsis*. However, the statistical support for these relationships is very weak (Meve & Liede 2002) and there appears to be no morphological support for it at all.

Richtersveldia columnaris

Richtersveldia columnaris (Nel) Meve & Liede,
Plant Syst. Evol. 234: 205 (2002).
Trichocaulon columnare Nel, *Kakteenkunde* 1933:135
 (1933).
Echidnopsis columnaris (Nel) R.A.Dyer & D.S.Hardy,
Cact. Succ. J. (US) 40: 207 (1968).
Notechidnopsis columnaris (Nel) Lavranos & Bleck,
Cact. Succ. J. (US) 57: 256 (1985).
Type: South Africa, Cape, Hellskloof, Sept. 1929,
Herre sub SUG 6023 (BOL).

Richtersveldia

Richtersveldia Meve & Liede, *Plant Syst. Evol.* 234:
 204 (2002).
Type: *Richtersveldia columnaris* (Nel) Meve & Liede.



Fig. 14.1. Distribution of *Richtersveldia columnaris*.

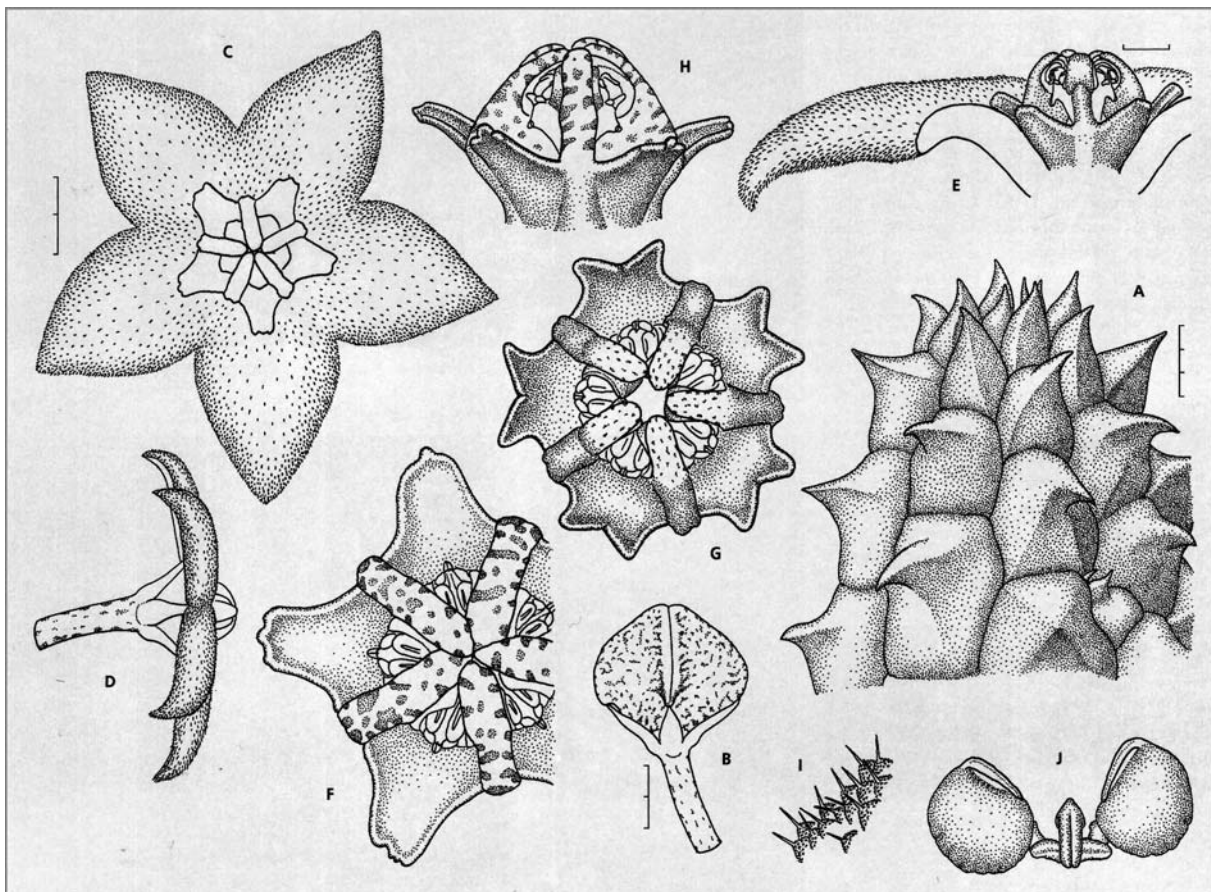


Fig. 14.2. *Richtersveldia columnaris*. A, apex of stem. B, bud. C, face view of flower. D, side view of flower. E, side view of dissected flower. F, G, face view of gynostegium. H, side view of gynostegium. I, papillae inside corolla. J, pollinarium. Scale bars: A, D, 3 mm (at A); B, 2 mm; C, 2 mm; E, 1 mm; F, G, 0.5 mm (at E); H, 1 mm (at A); I, 0.5 mm (at A); J, 0.25 mm (at A). Drawn from: A, G, J, PVB 4720, west of Eksteenfontein; B, D, E, PVB 1323, top of Hellskloof, Richtersveld; C, F, H, I, Hardy 456, top of Hellskloof.

Succulent forming loose clump to 600 mm diam. or with widely scattered stems connected beneath the soil by rhizomes, branching mainly at base. **Stems** 80-200 (-600) mm long, 20-25 mm thick, decumbent and frequently rhizomatous, with erect above-ground portions, greyish green; **tubercles** 3-5 mm long, prominent, hexagonal, joined towards bases into 8 broadly obtuse angles along stem, tapering to acuminate spreading tooth. **Inflorescences** many per stem in upper two thirds, each with (1-) 5-20 flowers opening often in rapid succession, arising from persistent peduncular patch sometimes reaching 10 mm long; **pedicel** 2-4 mm long, < 1 mm thick, spreading with flower facing horizontally, finely papillate; **sepals** 2 mm long, $\pm$ 1 mm broad at base, ovate-lanceolate, green with reddish brown spots, finely papillate. **Corolla** 10-) 12-17 mm diam., rotate to reflexed; outside pale green, spotted finely with red, with scattered bristle-like papillae, otherwise glabrous and smooth; inside greenish yellow with purple-red dots, covered with conical-obtuse papillae each tipped with an acute bristle (up to 0.25 mm long); **tube** shallow, V-shaped, containing lower half of gynostegium; **lobes** 3.5-4.5 mm long, 2.5-3.5 mm broad at base, spreading, ovate-deltate to ovate-lanceolate, with apices and margins slightly recurved. **Corona** 4 0-4.5 mm diam., consisting of 2 series of lobes arising on staminal tube and partly intergrown; **outer lobes** $\pm$ 1.5 mm long, ascending, truncate, bright yellow with red blotches, fused laterally in lower third with dorsal projections of inner lobes into broad cup containing only lower third of column; **inner lobes** $\pm$ 1 mm long, adpressed to backs of anthers, dorsiventrally flattened, broadly linear, obtuse, yellow dotted with purple-red, with small obtuse dorsal projection in series with and laterally fused to outer lobes. **Anthers** horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** ellipsoidal, longer than broad, insertion-crest exactly along outer edge, caudicle attached with small $\pm$ circular pad to ventral surface. **Follicles** erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

Distribution and habitat

Richtersveldia columnaris is endemic to the north-western corner of Namaqualand. Here it has a restricted distribution in the westernmost high ridges of the Richtersveld from Koda's Peak in the north to Eksteenfontein, where it occurs at altitudes of 500-800 m. It has not been recorded north of the Orange River and is one of the few stapeliads which is endemic to the Richtersveld.

Plants are usually found on steep, rocky slopes or on stony summits in short scrub consisting mainly of succulents where they grow inside bushes or between rocks. On several occasions they have been found to be locally very common.

Diagnostic features and relationships

In *R. columnaris* many of the stems spread horizontally first beneath the soil for 300 mm or more. When they emerge, they become thicker and erect. The above-ground parts are mostly not more than 300 mm tall but odd stems up to 600 mm long do occur, particularly if they grow in dense shade. Because of the rhizomatous habit of the stems, the plants do not form dense clumps and are mostly rather diffuse. Here the stems are almost cylindrical and somewhat snake-like, with the short, quite sharply conical tubercles arranged into eight low but very clearly defined angles.

In *R. columnaris* the primary stem does not bear flowers and these arise only on the side-branches. They appear on many small, peduncular patches mainly towards the tips of new growth, although older inflorescences may be re-activated to produce flowers, so occasionally, they can be found lower down on stems too. The lowest bract looks very much like a normal tubercle but with a flattened upper surface.



Fig. 14.3. *R. columnaris*, PVB 1321, top of Hellskloof, Richtersveld.



Fig. 14.4. *R. columnaris*, PVB 7321, foot of Vandersterrberg, near Kubus, Richtersveld.

In this species often a whole cluster of flowers on a patch will open simultaneously. The small, greenish yellow flowers are flat to slightly convex and are usually finely and indistinctly spotted with red. The interior is densely covered with small papillae, each of which has an apical bristle.

There is only a very slight tube in the centre, so the corona projects somewhat from the centre of the flower. It is yellow mottled with red and consists of small outer lobes more or less adpressed to the corolla around the mouth of the tube and small inner lobes adpressed to the backs of the anthers.

History

Richtersveldia columnaris was first collected by Rudolf Marloth on 28 August 1925 near Kubus in the Richtersveld. He annotated his material as '*Trichocaulon hospitans*' (Latin: *hospitans* = strange, foreign) and was possibly quite unsure where to place the species, but he never published this name. Nel described *Trichocaulon columnare* from material collected by Hans Herre in September 1929 at Hellskloof. This species was also regarded as very rare by Hall (1957), but it is actually only relatively local in its occurrence and is really quite common where it occurs.



Fig. 14.5. *R. columnaris*, PVB 9135, north of Lekkersing, showing the rhizomatous stems (all belonging to one plant), growing under a much-grazed shrub of *Euphorbia rhombifolia*.

15. Stapelia



The generic name *Stapelia* was first coined by Linnaeus early in 1737 in *Genera Plantarum*. This book was the first step towards the binomial system which he formally introduced in 1753 and in it the entities listed under the genera did not have specific names. Under *Stapelia* there seems to be only one species referred to and this was based on an illustration of Paul Hermann. This is what later became *Stapelia variegata*, having been referred to as *Fritillaria crassa* by Johannes Bodaeus Å Stapel (1644). In Linnaeus' *Hortus Cliffortianus*, which also appeared in 1737, *S. variegata* is

listed first, followed by a second taxon with pubescent stems. He named the genus for Johannes Bodaeus A Stapel, a Dutchman who had 'detected' the first species (see under *Orbea variegata*). This was, in fact, not the first name given to these plants. The earliest generic name for them was *Crassa*, which was published in 1718 by Heinrich Bernhard Ruppini and included both *S. variegata* and *S. hirsuta*. Also in 1730 Lorenz Heister baptised them *Stissera* (in honour of L.A. Stisser). Linnaeus even used the name *Stissera* in his first edition of *Systema Naturae* (of 1735) but by 1737 he had abandoned it in favour of *Stapelia*. Otto Kuntze's attempt (1891: 421) to replace *Stapelia* by *Stissera* fortunately failed.

In *Species Plantarum* of 1753, Linnaeus listed two species of *Stapelia*, *S. variegata* and *S. hirsuta* (again in that order). Although a few others came to be known during his lifetime, Linnaeus only described one more, namely *S. mammillaris* in 1771, and it was his son who described the next two known species, namely *S. incarnata* and *S. pilifera*. The genus increased dramatically in size with the 37 new species described by Francis Masson in 1796-8. These were the plants that he discovered during his two sojourns at the Cape, when he explored

extensively in the arid parts of the colony, on some occasions together with Thunberg.

At this stage all the leafless succulent asclepiads with angled stems and clear sap were placed in *Stapelia*. In 1810 Robert Brown proposed that the genus be divided and that various species be placed in three new genera: *Caralluma*, *Huernia* and *Piarranthus*. A.H. Haworth seems to have strongly supported this idea and proposed further subdivision, creating the additional new genera *Caruncularia*, *Duvalia*, *Gonostemon*, *Obesia*, *Orbea*, *Podanthes*, *Tridentea* and *Tromotriche* and leaving a rather miscellaneous assemblage

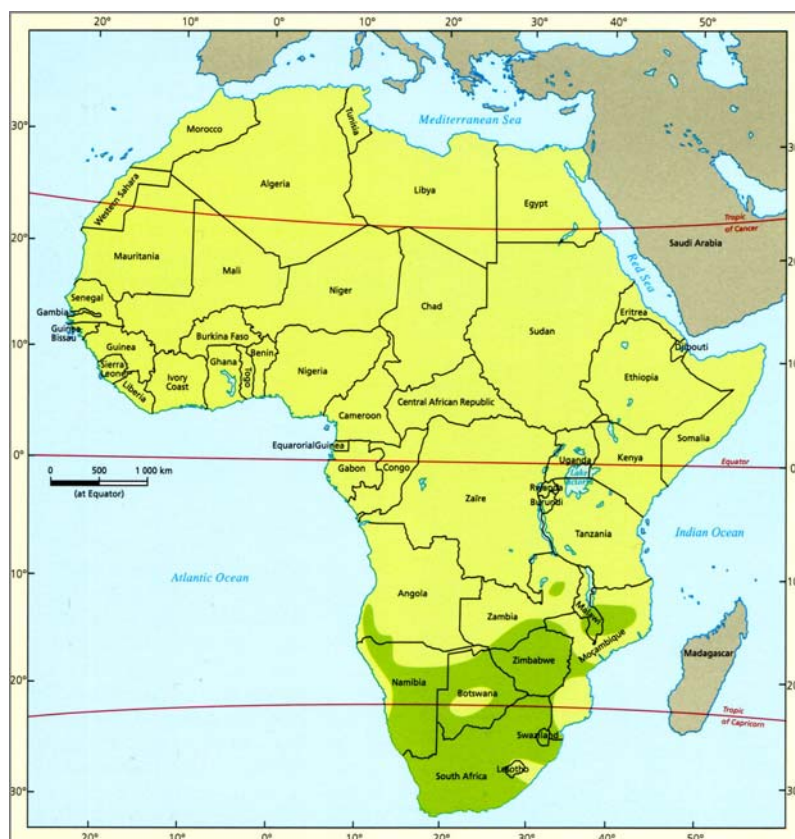


Fig. 15.1. Distribution of *Stapelia* in southern Africa.

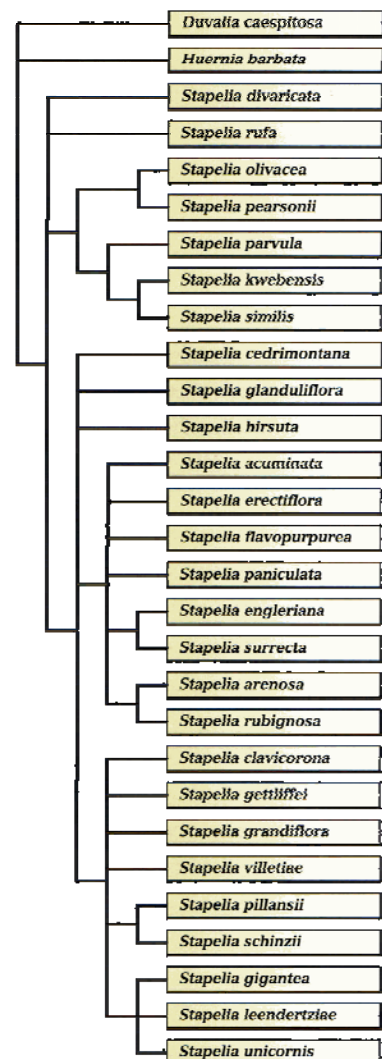


Fig. 15.2. Simplified cladogram derived from morphological characters showing the possible relationships among the species of *Stapelia*.

of 31 species in *Stapelia* (Haworth 1812). This he subdivided again, into four groups (one of which remained unnamed). Later (in 1819) he moved one other species (*S. articulata*) to a further new genus, which he called *Pectinaria*. Today one may well wonder why he kept such a curious mixture of names as *Stapelia hirsuta*, *S. mammillaris* (now *Quaqua mammillaris*) and *S. pilifera* (now *Hoodia pilifera*) under *Stapelia*. However, it seems that he was very aware of the failings of his system and he expressed regret that he had had insufficient time to study them and had grown only very few of them (Haworth 1812). Indeed, several of them must at that time have been extremely difficult to obtain in the living state, for there were very few travelers who ventured into the still relatively unknown interior of southern Africa and plants that were collected also had to survive the rigors of a long journey by ship back to Europe. Haworth's many new genera met with little contemporary favour. J.A. Schultes (1820) returned them all to *Stapelia* (with the single exception of *Pectinaria*) and this was followed by Stephan L. Endlicher

(Endlicher 1836-40), though this fate was not suffered by any of Robert Brown's genera. Both of these authors maintained many of Haworth's segregate genera as informal sections of *Stapelia*. This position was followed by the Belgian botanist Joseph Decaisne (Decaisne 1844), although he even returned *Pectinaria* to *Stapelia*. Decaisne recognised 10 sections of *Stapelia* and was the first to validate their status as sections.

N.E. Brown of Kew described many species of *Stapelia* and was the first person to consider seriously once more the possibility of moving species out of *Stapelia* (Brown 1890). He refined the concepts of several of the other genera which had been proposed (such as *Caralluma*, *Duvalia*, *Huernia* and *Piранthus*) and in many of these cases his refinements still characterise these genera. He also described several new genera and moved many species of *Stapelia* to them. Within *Stapelia* he recognised the close vegetative similarities between *S. aperta* and *S. pedunculata* and between *S. ciliata* and *S. namaquensis* but, in line with the Linnaean tradi-

tion, he felt that substantial differences in floral characters excluded the possibility that these taxa could belong to the same genera. For this and other reasons, he again left a substantial miscellany of species in *Stapelia*.

While Brown was certainly familiar with these plants to a level that had never before been the case and, while he knew enough about them to appreciate how variable they were (Brown 1890: 3), he had no field experience at all. Detailed field experience and a herbarium record based more closely on this experience has shown that a considerable number of the names which N.E. Brown, Alwyn Berger and White & Sloane spent many pages describing in great detail did not refer to species which could be identified in the wild. Many represented hybrids, of which a few had themselves been collected in habitat but most of which had arisen in cultivation (Berger 1910). Once these often confusing names had been removed, a clearer picture emerged and it was found that some of the vegetative similarities observed by Brown (and possibly even by Haworth) were

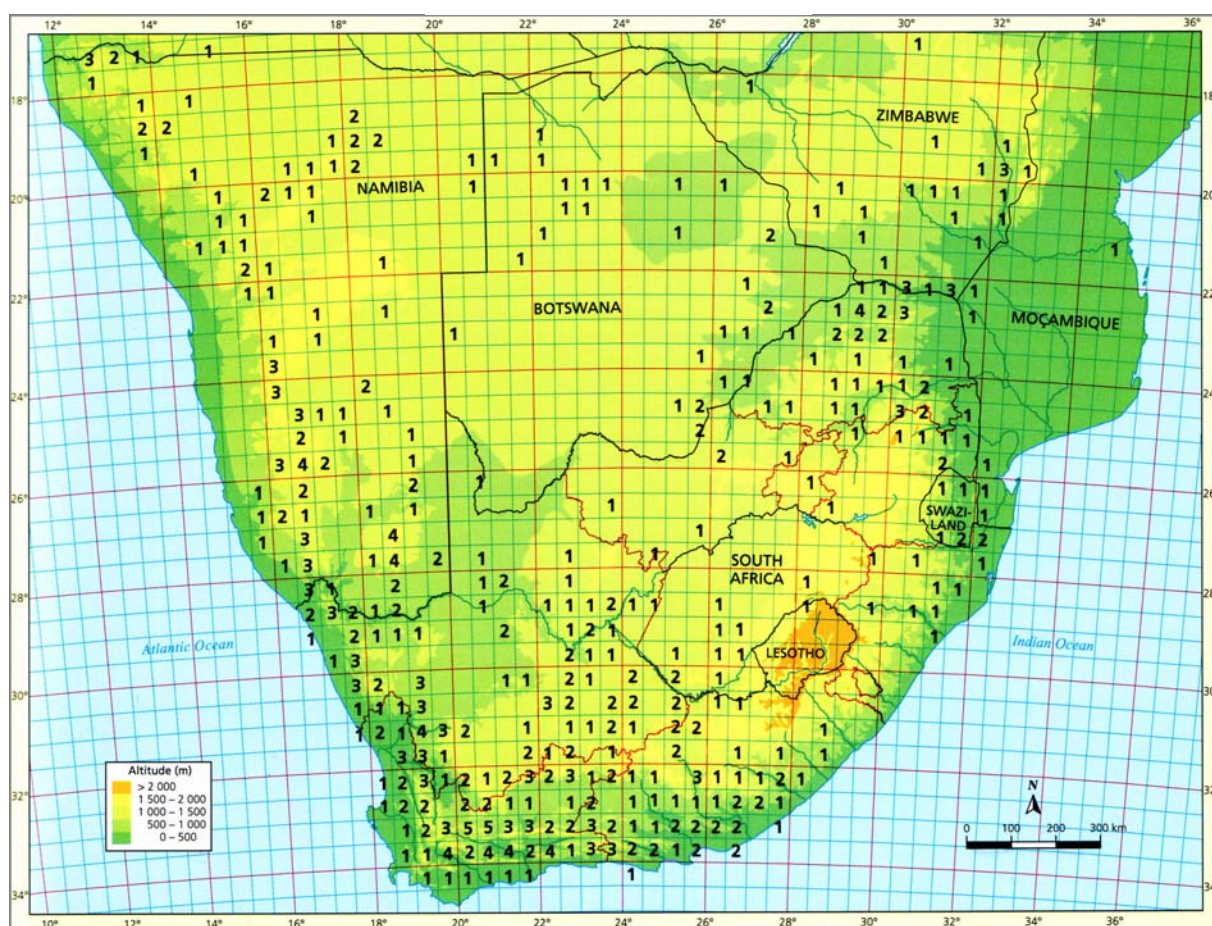


Fig. 15.3. Patterns of diversity in *Stapelia* in southern Africa, showing the number of species recorded to date in each half-degree square.

STAPELIA

actually of deeper significance. Leach (1975) was the first to re-examine the position and to begin the process of excising groups of related species from *Stapelia* with the resurrection of Haworth's *Orbea*. He soon followed this with the re-instatement of the long disused generic names *Tridentea* and *Tromotriche*, both of which contained species formerly in *Stapelia*.

White & Sloane recognised 99 species in *Stapelia* (which they divided into 10 sections) but, since many of these have now been moved to other genera, this is not very informative. Leach (1985) recognised 43 species in *Stapelia* (but did not subdivide the genus at all) and so, with the moving back to *Stapelia* of *Tromotriche engleriana* (Bruyns 1995a), the total was raised to 44. Leach took a broad view of the complex surrounding *S. grandiflora* and hinted in several places that he might have done the same in the complex around *S. hirsuta* if more material had been available. Here a broad view is taken of *S. hirsuta* as well as of the small-flowered species related to *S. paniculata* where it has proved impossible to distinguish between many of the taxa that he recognised. In this account, *Stapelia* is considered to have 29 species, which is made up of 28 species in southern Africa (including *S. remota*) and one, *S. parvula*, in southern Angola, outside the region treated in this book.

Recent molecular investigations (Meve & Liede 2002) included *S. glanduliflora* and *S. rufa* and found that they formed a well-supported branch but of indeterminate relationships. Our own investigations added the large-flowered *S. gigantea* and *S. engleriana*. Our analyses show that neither of these group with the other two, but this is most likely to be due to the absence of phylogenetically informative characters and may be resolved by looking at further gene regions.

Stapelia L., *Sp. PL* 1: 217 (1753).

Stapelia sect. *Stapeltonia* Decne, in DC, *Prodr.* 8:

652 (1844), *nom. superfl.*

Gonostemon subg. *Stapeltonia* (Decne.)

P.V.Heath, *Caiyx* 3: 7 (1993).

Lectotype: *Stapelia hirsuta* L.

Gonostemon Haw., *Syn. PL Succ.*: 27 (1812).

Stapelia [unranked] *Gonostemon* Schult. in

Roem.& Schult., *Syst. Veg.* 6: 27 (1820).

Stapelia sect. *Gonostemon* (Haw.) Decne. in DC,

Prodr. 8: 655 (1844).

Lectotype: *Gonostemon divaricatus* (Masson) Haw.

[= *Stapelia divaricata* Masson].

Stapelia sect. *Fissirostres* N.E.Br., *Hooker's Icon. PL*

20: 10 (1890).

Gonostemon subg. *Nelia* P.V.Heath, *Calyx* 3: 9 (1993).

Lectotype (selected here): *Stapelia fissirostris* Jacq.

[= *Stapelia rufa* Masson].

Gonostemon subg. *Clavicornona* P.V.Heath, *Calyx* 3:

8 (1993).

Type: *G. clavicornona* (L.Verd.) P.V.Heath [= *Stapelia clavicornona* L.Verd.].

Gonostemon subg. *Kersia* P.V.Heath, *Calyx* 3: 9

(1993).

Type: *G. kwebensis* (N.E.Br.) P.V.Heath.

Gonostemon subg. *Massonia* P.V.Heath, *Calyx* 3: 9

(1993).

Type: *G. concinnus* (Masson) P.V.Heath [= *Stapelia concinna* Masson].

Spineless rarely rhizomatous (*S. engleriana* only) succulent forming compact to diffuse clumps up to 2 m diam. **Steins** 20-300 mm long, 4-25 mm thick, erect to decumbent (prostrate only in *S. engleriana*), fleshy and firm (often flaccid in *S. gettliffei*), pubescent or rarely almost glabrous, green to reddish green sometimes mottled with purple or red; **tubercles** 1-5 mm long, laterally much flattened and fused into 4 (rarely 5 or 6) obtuse often wing-like angles along stem with concave area between angles, each bearing at their apex (usually near upper end relative to stem) a small erect deltoid to lanceolate caducous leaf-rudiment 1-11 mm long subtended laterally by small persistent stipular glands. **Inflorescences** pubescent (rarely ± glabrous), 1-3 (-6) per stem, arising at all heights along stem, each bearing 1-5 flowers developing in gradual succession from short stout peduncles (mostly < 10 mm, rarely up to 30 mm long), with several short deltoid bracts 1-2 (-5) mm long without lateral teeth; **pedicel** 3-80 (-120) mm long, 1.5-4.0 mm thick, ascending to spreading; **sepals** 2.5-10 (-15) mm long, 1-3 mm broad at base, lanceolate to ovate, acute. **Corolla** (6-) 8-200 (-400) mm diam., rotate to shallowly cupular, rarely campanulate (often urceolate in *S. leendertziae*), mostly deeply lobed (except in *S. leendertziae*); outside finely pubescent, usually with darker (not outstanding) veins on lobes; inside usually transversely rugulose, usually hairy (sometimes densely so); **tube** usually very short (< 5 mm long) and strongly pentagonal around base of gynostegium, sometimes shallowly bowl-shaped beyond this (*S. leendertziae*); **lobes** (3-) 8-100 mm long, (3-) 5-35 mm broad at base, spreading to reflexed, deltate or ovate to narrowly lanceolate, convex above from mostly strongly recurved margins usually with fine cilia (only rarely vibratile). **Corona** 2.5-19.0 mm tall, 5-15 mm broad, consisting of 2 series arising on staminal tube and slightly intergrown only near bases, outer very slightly below inner, glabrous (pubescent in 3 species), raised above base of tube on stout pentagonal stipe 1-2 mm tall; **outer lobes** ascending to spreading, simple (rarely bifid at apex), channelled down upper surface; **inner lobes** adpressed to backs of anthers for most of anthers' length, mostly exceeding them and meeting in centre or rising connivent and then diverging, dorsiventrally flattened towards base, becoming slender and terete above (rarely clavate: *S. clavicornona*, *S. engleriana*), mostly with conspicuous laterally flattened dorsal appendage arising near base and often as long as lobe. **Anthers** horizontal on top of style-head, margins usually shrinking back to expose pollinia, rectangular to obtriangular. **Pollinium** D-shaped, insertion-crest twisting from outer edge to dorsal surface, caudicle attached with broad cupular pad to base. **Follicles** erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, pubescent, smooth.

Plants of *Stapelia* form dense to diffuse clumps which may reach 1 m or considerably more in diameter. The stems are almost always erect from a short, horizontal base: the most obvious exceptions to this are their often laxly ascending habit in *S. gettliffei* and their frequently prostrate habit in *S. engleriana*. *Stapelia engleriana* is also the only species where they may be somewhat rhizomatous: in all others the bases of the stems remain on the surface of the soil, without spreading by underground rhizomes at all. In most species the stems are uniformly greyish green to reddish, depending on the extent of their exposure to sun. Only rarely are they mottled with red or purple on green; this happens, for example, in *S. schinzii* and in some of the almost glabrous-stemmed forms of *S. hirsuta*. There is a small group of species (*S. kwebensis*, *S. olivacea*, *S. pearsonii* and *S. similis*) where the stems are greyish with darker purple in the grooves between the angles.

One of the striking phenomena within *Stapelia* is the extent to which the stems vary in thickness. While this is nearly matched in large genera like *Orbea* and small genera like *Stapeliopsis*, it contrasts strongly with *Huernia*, where the stems vary relatively little in thickness. In *S. parvula*, *S. similis* and *S. paniculata* the stems may be less than 5 mm thick, whereas they are largest in *S. clavicornona* and *S. grandiflora*, reaching a diameter of 50 mm.

Tubercles on the stems are laterally flattened and joined vertically into continuous rows, usually with a conspicuously concave area between them. There are almost always just four of these rows per stem and, although 5-angled stems do occur, this is usually only as exceptions amongst other 4-angled ones. The rows themselves are variably conspicuous and range from thin and wing-like in such species as *S. clavicornona* and *S. gigantea* to almost obsolete in *S. pillansii* and *S. rufa*. Each tubercle bears a small leaf-rudiment which is usually positioned not in the middle of the tubercle (relative to the axis of the stem) but just beneath the base of the next tubercle. These leaf-rudiments vary from very tiny (e.g. about 1 mm long in *S. flavopurpurea* and *S. pearsonii*) to relatively conspicuous (up to 11 mm long in *S. gettliffei*) and they are erect when alive (i.e. parallel to the axis of the stem) but soon die off and wither away to leave a round scar at the tip of the tubercle. In some of them the slightly thickened midrib can be made out with a somewhat thinner blade flanking it. Around its base each leaf-rudiment has a pair of small, more or less spherical, glandular stipular denticles which tend to persist longer than the leaf-rudiment itself (fig. 17 A).

The surface of the stem in *Stapelia* is usually 'pubescent' and in Bruyns (1995a) it was shown that this pubescence is caused by the elongation of the outer walls of many of the epidermal cells into slender papillae (fig. 18 G). The cells

surrounding the base of a papilla are often raised into a mound but the cells between the elongated ones all have flat outer walls. There is a great deal of variation in the length of these papillae. In species such as *S. gettliffei* and *S. unicornis* individual papillae are clearly visible to the naked eye and the stems are coarsely velvety ('pubescent' in the descriptions that follow). In the majority of species they are more finely velvety ('shortly pubescent') while in yet others the stems give the appearance of being glabrous ($\pm$ glabrous in descriptions) and may even be slightly shiny (*S. divaricata*, some forms of *S. hirsuta*, *S. obducta*, *S. remota* and *S. schinzii* - see fig. 18 F). These 'glabrous' stems have a finely sandpapery texture and are never smooth and shiny as in species of *Tridentea*. On close examination, they turn out to have the same papillae but these are much shorter (and very similar to those found in *Tromotriche*), although longer ones such as in the 'shortly pubescent' species often lurk in corners, such as around the bases of the leaf-rudiments.

In *Stapelia* the flowers arise in a wide variety of positions along the stem (fig. 22 B, C). Species with larger flowers generally bear them near the base of the stem and then each stem has only one inflorescence, which sometimes bears only one flower. In smaller-flowered species the inflorescence may be near the base of the stem (as in *S. similis*) but often inflorescences are dispersed at various heights between the base and the apex (e.g. *S. arenosa*) and in these cases there may be up to six of them on one stem. The flowers generally open in gradual succession on an inflorescence. In all species the peduncle (which is usually short), the pedicels and the sepals are pubescent with the same kind and size of papillae as are found all over the stems.

The flowers in *Stapelia* are extremely variable in size. The smallest are found in the Angolan *S. parvula*, where they may be as little as 6 mm across, while the largest are encountered in *S. gigantea* where they may reach 400 mm in diameter. This size is only rarely exceeded elsewhere in the plant kingdom (Endress 1994) and no other genus of stapeliad exhibits anything like this range. However, in contrast, there is relatively little variation in the shape of the flower and it is invariably more or less flat and deeply lobed. Only in *S. leendertziae* and occasionally in *S. unicornis* is there a significant 'corolla tube' and in *S. leendertziae* the flowers are deeply campanulate to almost urceolate.

Perhaps more than in any other stapeliads, the flowers of *Stapelia* are renowned for their bad odours. While there is no denying that this reputation is well earned among the large-flowered species, what is interesting is that even in small-flowered ones such as *S. similis*, the flowers have a putrid odour which is quite strong for the size of the flower.

It is less well known, however, that there are actually species of *Stapelia* whose flowers are sweet-smelling, examples being *S. erectiflora* and *S. flavopurpurea*.

Mostly, the corolla has relatively long lobes and a small, rotate to slightly cupular, central, united area. Around the gynostegium there is always a very small, shallowly V-shaped corolla tube (broad with a flat base in *S. engleriana*) around whose mouth the corolla is noticeably thickened into an obscure annulus and then becomes thinner once more. The annulus is thick and projects somewhat forwards into the corolla tube in *S. divaricata* but it is hardly noticeable at all in species like *S. surrecta*. In such species as *S. leendertziae* and *S. rufa*, this annulus lies near the base of the apparent 'corolla tube' and thus the 'corolla tube' is made up of two distinct tubes: the 'primary' tube beneath the annulus and the 'secondary' tube beyond the annulus created by postgenital fusion of the lobes, as in many species of *Hoodia* and *Huernia*.

The surface of most *Stapelia* flowers is characteristic. Outside it is always papillate in the same manner as the stems, although this can be very hard to see in some cases. Inside it is usually transversely rugulose. These rugosities are very variable so the surface varies from nearly smooth in such species as *S. divaricata*, *S. erectiflora*, *S. pillansii* and *S. surrecta* to deeply and coarsely rugose as in *S. flavopurpurea*, *S. olivacea* and *S. similis*. In several species, particularly the large-flowered ones, the rugosities are paler than the rest of the corolla and they are usually yellow to cream against a background of red to purple-black. There are usually fine, cylindrical, unicellular hairs over much of the inside of the flower (fig. 28 F, G) and sometimes these have a constricted base. In several species, such as *S. similis*, these are absent. They have an unusual clavate shape in *S. erectiflora*, *S. glanduliflora*, *S. remota* (fig. 28 H) and *S. flavopurpurea* (in the last two only below the bases of the lobes) but are otherwise always slender. In the corolla tube around the base of the gynostegium there are often hairs, even when the rest is more or less glabrous, which are sometimes short and stout and adpressed to the surface. These tend to fill up the tube around the stipe of the gynostegium and seem to block access to this area. Towards the margins of the lobes, where any rugulosities generally subside, the hairs often become longer and also frequently arise from a raised papilla. Marginal cilia of the vibratile type (which are initially swollen and later dry out, as in fig. 25) are rare in *Stapelia* and are only known in *S. clavicorona*, *S. pillansii* and *S. schinzii*.

In *Stapelia* the gynostegium is always raised above the base of the tube on a pale, pentagonal stipe (fig. 30 A, B). Two series of corona lobes are present, with the outer lobes beneath the

guide-rails and the inner lobes adpressed to the backs of the anthers. In particular, the outer series does not spread at all around the gynostegium below the inner, nor are the two series vertically separated on the gynostegium as in *Huernia* and *Duvalia*.

In the flower of a typical *Stapelia* like *S. hirsuta*, the outer corona lobes are rectangular and relatively narrow with a slightly reflexed tip and are channelled above and slightly convex below. Towards the base the channel forms a shallow hollow beneath the guide-rail and runs into a shallow nectarial cavity towards the centre of the flower. The lobes vary considerably in length and may be deltoid rather than rectangular. In *S. kwebensis* and *S. similis* they are especially short (but remain broad), in which case a much deeper nectarial cavity than normal, with a considerably restricted entrance, develops near their base (fig. 30 B).

The inner lobes are very variable in length (much more so than the outer) but are always adpressed to the backs of the anthers. They are strongly dorsiventrally flattened over the anthers (though often cylindrical above and clavate there in two species) and usually have a laterally flattened dorsal horn near the base. This dorsal horn usually has a fin-like shape and is very variable in length. In the case of *S. clavicorona*, the base of the dorsal horn is still clearly laterally flattened but above this it is modified into a swollen lobule very similar in shape to the lobe itself. Such modifications are also found in several species of the closely related genus *Tromotriche*.

The pollinaria in *Stapelia* are comparatively large and always have somewhat D-shaped pollinia, with the insertion-crest twisted onto the dorsal surface from the outer edge (as in fig. 32 D).

A further distinctive characteristic of *Stapelia* is the fact that the follicles are pubescent in the same manner as the stems. These follicles can contain very large numbers of seeds and, in one pair on *S. pillansii*, 691 seeds were counted. The seeds are always boat-shaped (i.e. quite long and narrow and with the margins distinctly raised up to surround the central area) and they have comparatively thin margins (fig. 39 D).

Stapelia is found in Africa south of the equator (fig. 15.1), with the species mainly concentrated in Botswana, Zimbabwe and especially in Namibia and South Africa. Outside this region there is a small area in southern Angola where they occur and otherwise there are scattered collections from northern Zambia and southern Malawi as well as from certain parts of central Mocambique. Leach also cited two collections of *S. gigantea* from southern Tanzania and Kenya but, as these might both have been made from plants that escaped from cultivation, they have been left off the present distribution map.

Key to the species

1. Inner corona lobes distinctly clavate towards apices 2.
2. Stems $\pm$ prostrate, outer corona lobes much broader than dorsal horn of inner lobes, inner lobes 5–8 mm long, slenderly clavate with slender dorsal horn..... 15. *S. engleriana*
2. Stems erect, outer corona lobes about same breadth as dorsal horn of inner lobes, inner lobes $\pm$ 3 mm long, shortly clavate, each with more stoutly clavate dorsal process 25. *S. clavicorona*
1. Inner corona lobes cylindrical towards apices (not distinctly swollen there) or dorsiventrally flattened 3.
3. Corona lobes pubescent 4.
4. Corolla campanulate, inner corona lobes erect beyond middle of anthers and shortly bifid to truncate 1. *S. rufa*
4. Corolla rotate to somewhat reflexed, inner corona lobes adpressed to anthers and acuminate if rising above them, emarginate or truncate to acuminate 5.
5. Inner corona lobes acuminate and with spreading deltoid dorsal horn, corolla deeply rugulose on central rotate part 12. *S. arenosa*
5. Inner corona lobes truncate to emarginate and without dorsal horn, corolla only slightly rugulose on central rotate part 13. *S. rubiginosa*
3. Corona lobes glabrous 6.
6. Corolla lobes covered (especially towards margins) with erect to adpressed clavate hairs 7.
7. Pedicels erect holding corolla near or above apices of stems, inner corona lobes (2.5–) 3.0–3.5 mm long 8. *S. erectiflora*
7. Pedicels spreading with upturned apex holding flower facing upwards on ground, inner corona lobes 2.0–2.5 mm long 7. *S. glanduliflora*
6. Corolla lobes with simple (not clavate) hairs or $\pm$ glabrous 8.
8. Inner corona lobes not exceeding 3.5 mm long, often shorter than or only slightly longer than anthers 9.
9. Stems $\pm$ glabrous to the naked eye 10.
10. Corolla inside smooth and shiny to at most faintly rugulose towards centre, with fine cilia along margins of lobes but otherwise not pubescent 6. *S. divaricata*
10. Corolla inside rugulose over most of surface especially towards centre, somewhat shiny towards centre or dull, finely pubescent towards apices of lobes 16. *S. cedrimontana*
9. Stems shortly pubescent 11.
11. Outer corona lobes considerably broader than long and spreading, inner lobes arising somewhat above level of outer lobes, narrowly ovate to oblong-ovate, adpressed to anthers right to tips, without any trace of dorsal wing..... 12.
12. Pedicel at least 30 mm long (usually > 50 mm long), spreading with upturned apex holding flower facing upwards $\pm$ on ground 2. *S. similis*
12. Pedicel short (10–30 mm long) and spreading with flowers facing outwards from stems or to 50 mm long and erect with flower facing upwards 3. *S. kwebensis*
11. Outer corona lobes narrower than long, ascending-spreading, inner lobes arising $\pm$ at same level as outer, narrowly acuminate, adpressed to anthers but with erect to recurved tips, mostly with dorsal wing 11. *S. paniculata*
8. Inner corona lobes more than 4 mm long, always much exceeding anthers 13.
13. Corolla campanulate to urceolate with lobes shorter than depth of tube 23. *S. leendertziae*
13. Corolla rotate to shallowly campanulate with lobes much longer than depth of tube 14.
14. Corolla lobes with vibratile cilia along margins, mainly towards base 15.
15. Stems $\pm$ glabrous, often mottled with purple, corolla usually finely and densely rugulose inside (rarely very smooth and shiny) 27. *S. schinzii*
15. Stems shortly pubescent, uniformly coloured, corolla smooth inside but never shiny 26. *S. pillansii*
14. Corolla lobes without vibratile cilia 16.
16. Inside of corolla with clavate hairs on united part below lobes 17.
17. Corolla $\pm$ turban-shaped with broadly ovate lobes, inside mostly dark red or maroon, with small clavate hairs in dense patch around mouth of tube *S. remota*
17. Corolla rotate with narrowly ovate to lanceolate lobes, inside green yellow to pale red or brown with white centre, with lax covering of clavate hairs on united part 9. *S. flavopurpurea*
16. Inside of corolla with fine hairs or glabrous 18.
18. Leaf-rudiments 6–11 mm long, stems rather limp and trailing 20. *S. gettliffei*
18. Leaf-rudiments < 5 mm long, stems firm and mostly erect 19.
19. Outer corona lobes narrowly deltoid, inner lobes with slender dorsal horn $\pm$ as broad as thick 20.
20. Pedicel 30–40 mm long, corolla lobes narrowly ovate with revolute eciliate margins 5. *S. pearsonii*
20. Pedicel 4–6 mm long, corolla lobes ovate-deltate, with margins at most slightly recurved and mostly with many fine cilia 4. *S. olivacea*
19. Outer corona lobes $\pm$ parallel-sided with truncate to crenulate apex, inner lobes with broad dorsal horn much broader than thick 21.
21. Corolla facing upwards 22.
22. Flowers borne near apex of stem, pedicel 1.5–2.0 mm thick, corolla 22–40 mm diam., uniformly coloured, lobes without marginal hairs 14. *S. surrecta*
22. Flowers borne near base of stem, pedicel 3–4 mm thick, corolla 45–65 mm diam., purple-black with transverse yellow markings towards centre, lobes with marginal hairs 24. *S. villetiae*

(Continued on next page)

Key to the species (continued)

21. Corolla facing $\pm$ horizontally or adpressed to ground 23.
23. Corolla at most 50 mm diam 24.
24. Stems virtually glabrous 25.
25. Corolla lobes strongly reflexed at anthesis to give flowers turban-like shape 18. *S. obducta*
25. Corolla lobes not strongly reflexed, without turban-like shape 26.
26. Corolla transversely rugulose within, barred towards centre with yellow on red to maroon 16. *S. cedrimontana*
26. Corolla mostly $\pm$ smooth inside, usually uniformly red to maroon 17. *S. hirsuta*
24. Stems shortly pubescent 10. *S. acuminata*
23. Corolla > 50 mm diam 27.
27. Corolla lobes acuminate, with marginal hairs distichously arranged or somewhat pressed to surface, longer than those elsewhere on corolla 28.
28. Inner corona lobe with dorsal horn completely united with lobe, corolla 80–130 mm diam. 22. *S. unicornis*
28. Inner corona lobe with dorsal horn separated to near base from lobe, corolla 125–400 mm diam. 21. *S. gigantea*
27. Corolla lobes acute, with weak marginal hairs not different from those on rest of corolla 29.
29. Corolla usually only obscurely marked with cream or yellow on darker background, not deeply transversely rugulose, mostly glabrous in upper half of lobes 19. *S. grandiflora*
29. Corolla distinctly transversely rugulose with rugosities plainly marked with cream or yellow OR smooth and shiny, mostly pubescent in upper half of lobes 17. *S. hirsuta*

Within southern Africa (fig. 15.3), *Stapelia* is widely distributed but mainly concentrated around the mountainous edges of the subcontinent with only a single species (*S. kwebensis*, which is also the most widely distributed species of *Stapelia*) that is found right across the tropical part from the west near the Atlantic to near the Indian Ocean. The genus is most densely concentrated along the mountains from near Helmeringhausen in Namibia to the temperate western and southern parts of South Africa, with a further concentration in the mountainous north-eastern corner of the country. It is absent in the sandy central Kalahari, the most arid parts of the Namib and the wetter, highest parts of the Drakensberg. The number of species never rises above five in any half-degree square but there are several areas where four or five species per half-degree square are found. These are always in mountainous terrain: the Great Karas Mountains, the Tiras Mountains, the edge of the Nieuwoudtville Plateau and around the edges of the sandstone mountains of the Little Karoo, with a slightly lesser peak in the Baynes Mountains of northern Namibia. Most of the species are widely distributed (especially those occurring north of 30°S) and these peaks of concentration are mainly caused where several of these widely distributed taxa occur close to more local montane endemics (e.g. the very local *S. pearsonii* in the Great Karas Mountains meeting the widely distributed *S. kwebensis*, *S. schinzii* and *S. similis*; the local *S. clavicorona* in the Soutpansberg meeting the widely distributed *S. kwebensis*, *S. gigantea* and *S. gettliffei*). The peak around Matjiesfontein (in the half-degree squares 3320 A and 3320 B) is caused by taxa restricted respectively to the Ceres Karoo, Little Karoo and the Cape Fold Mountains all occurring close together (as happens also in *Quaqua*).

Stapelia has several very local species.

Of these, *S. clavicorona* grows in sandstone mountains [*Quaqua* also possesses sandstone endemics but these are restricted to the southern edges of the Great Karoo and the Little Karoo], while *S. pearsonii* is confined to the Great Karas Mountains of southern Namibia, and *S. divaricata* is restricted to dry, rocky spots on the coastal plain near Swellendam.

1. *Stapelia rufa*

Stapelia rufa Masson, *Stap. Nov.*: 16, t. 20 (1797).

Gonostemon rufus (Masson) P.V.Heath, *Calyx* 1:19 (1992).

Type: South Africa, Cape, beyond Platteklouf, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 20.

Stapelia rufescens Salm-Dyck, *Hort. Dyck.*: 373 (1834).

Type: unknown.

Stapelia fissirostris Jacq., *Stap.*: t. 23 (1806-19).

Stapelia rufa var. *fissirostris* (Jacq.) A.C.White & B.Sloane, *Stap.*, ed. 2, 2: 483 (1937).

Gonostemon rufus var. *fissirostris* (Jacq.) P.V.Heath, *Calyx* 3: 9 (1993).

Lectotype: Jacq., *Stap.*: t. 23.

Stapelia rufa var. *attenuata* N.E.Br., *Fl. Cap.* 4 (1): 966 (1909).

Gonostemon rufus var. *attenuatus* (N.E.Br.)

P.V.Heath, *Calyx* 3: 9 (1993).

Lectotype: between Muiskraal and Ladismith, N.S. Pillans 685 (K, holo.; BOL, iso.).

Small succulent forming compact clump 50-500 mm diam.

Stems 60-120 mm long, 10-15 mm thick, erect, shortly pubescent, green suffused with purple (not mottled); **tubercles** up to 2 mm long, widely spaced along stem and very obscure, obtusely conical, joined into 4 broadly obtuse angles along stem and stem $\pm$ roundedly square in cross-section; **leaf-rudiment** 1.5-2.5 mm long. **Inflorescences** pubescent, 1 per stem usually near base, with 1-5 (-8)

flowers opening in fairly quick succession on short stout peduncle < 5 mm long, with few subulate bracts 1-2 mm long; **pedicel** 4-8 mm long, 1.5 mm thick, spreading and holding flower facing horizontally; **sepals** 3-4 mm long, 1.5-2.5 mm broad at base, narrowly lanceolate, acute. **Corolla** 30-15 mm diam., campanulate; outside greenish, with 3-5 darker veins on each lobe; inside finely transversely rugulose, yellow to pinkish or red-brown or purple-brown, sometimes paler between rugosities and in base of tube, with fine sharp-tipped papillae on rugosities in upper half of lobes and along margins where reaching 1 mm long towards base (also few in base of tube); **tube** $\pm$ 1 mm long, 10 mm broad, longer than gynostegium, pentagonal, widening from flat base gradually towards mouth (at base of lobes), corolla thickest $\pm$ at level of outer corona lobes; **lobes** 15-20 mm long, 6-8 mm broad at base, ascending to spreading often with incurved tips, ovate, acuminate and often caudate, slightly convex above from recurved margins. **Corona** $\pm$ 4 mm tall, $\pm$ 4-5 mm broad, raised on obtusely pentagonal stipe 1.5-2.0 mm long, sparsely pubescent towards tips of inner lobes; **outer lobes** 1.0-1.5 mm long, 1.0-1.5 mm broad, spreading, $\pm$ square with deltoid apex, acute to obtuse, slightly channelled above (more towards base), yellow to orange or orange-brown; **inner lobes** 1.5-2.0 mm long, adpressed to backs of anthers in lower half then erect and sometimes slightly recurved above, dorsiventrally flattened, $\pm$ rectangular, shortly bifid to truncate, sometimes dorsally slightly swollen towards base, red-brown to black.

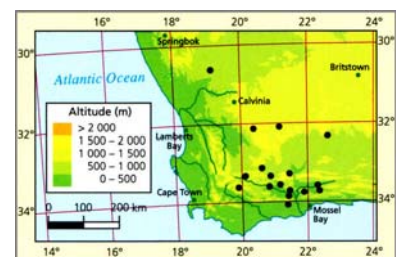


Fig. 15.4. Distribution of *Stapelia rufa*.

STAPELIA RUFA

Distribution and habitat

Stapelia rufa is of fairly wide but scattered occurrence in the Little Karoo from the Warmwaterberg to Ladismith and to south-east of Oudtshoorn but it also grows between Touws River and Laingsburg on the northern boundary of this area. There are several other widely scattered localities (such as north-west of Loeriesfontein, several records in the Roggeveld from near Middlepos and near Fraserburg) and these do not fit into the pattern of a Little Karoo element at all. The collection cited by Leach (1985) from Beaufort West is therefore not beyond the bounds of possibility but that from near Prieska seems unlikely and has been omitted from the map.

Plants generally grow on stony, north-facing slopes among bushes and between rocks.

Diagnostic features and relationships

Although some large plants of *S. rufa* have been encountered, specimens are usually small, perhaps reflecting the harsh conditions under which they often grow and the longevity of the plants under these straitened circumstances.

The stems are usually 4-angled and noticeably rounded in cross-section since the angles hardly project from the surface and there are more or less no grooves between them. In this respect they are similar to those of *S. pillansii* but are immediately distinguishable from those of *S. hirsuta*, with which they frequently occur.

Florally *S. rufa* can be mistaken for no other species. The fairly small flowers are usually not more than 40 mm across and are borne in small clusters near the bases of the younger stems. In cultivation they are almost always produced in spring and do not flower in autumn as do nearly all other species of *Stapelia*. They have an obvious, often broad and shallow tube in



Fig. 15.5. *S. rufa*, PVB 4806, south-west of Fraserburg. An unusual yellow-flowered form found by A.S. Theron on his farm.



Fig. 15.6. *S. rufa*, PVB 7511, west of Barrydale.

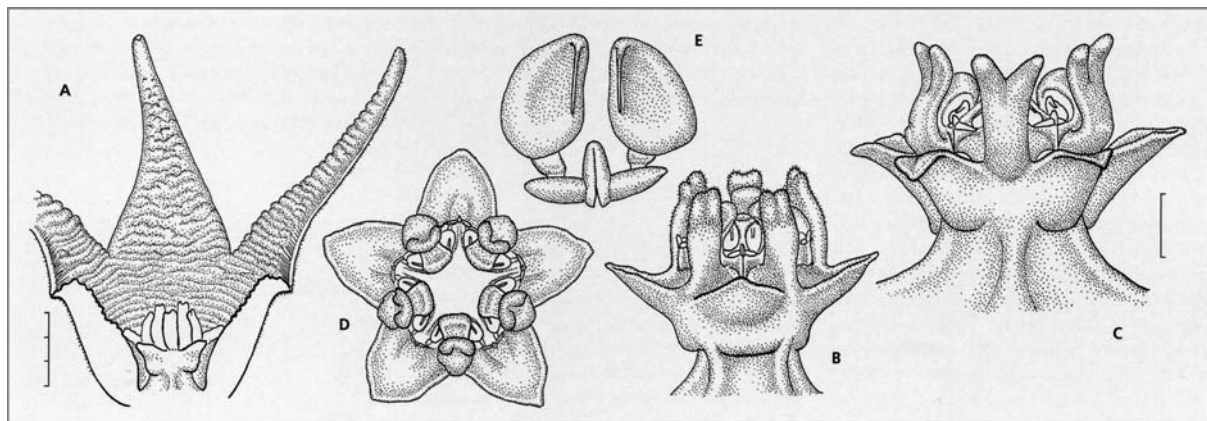


Fig. 15.7. *Stapelia rufa*. A, side view of dissected corolla. B, C, side view of gynostegium. D, face view of gynostegium. E, pollinarium. Scale bars: A, 3 mm; B-D, 1 mm (at C); E, 0.25 mm (at A). Drawn from A, B, D, E, PVB 2532, Langeberg, north-west of Loeriesfontein; C, PVB 4818, south-east of Konstabel.



Fig. 15.8. *S. rufa*, PVB 4567, south-west of Rooinek Pass, near Laingsburg.

the centre in which the walls become thicker, reaching their maximum just below the outer corona lobes. After this they become thinner once more so that towards the base the tube broadens slightly and the base on which the gynostegium stands is then more or less flat. The lobes spread widely tapering into a slender tail from a broader base. The interior is finely and quite densely transversely rugulose right down to the thickened part of the tube where these ridges abruptly stop and the surface is smooth. There are small 'hairs' towards the tips of the lobes. Hairs are also present along the margins of the lobes, mainly in their lower half. The flowers are usually red-brown (whence the name) but may be pinkish or even, occasionally, yellow and they always emit an unpleasant odour.

The gynostegium is entirely contained within the corolla tube but stands up above the base on a reasonably tall stipe. It has small, roughly square outer lobes, which are yellow or orange. In *S. rufa* the inner corona lobes are quite unusual, being more or less erect and much darker, often nearly black, than the outer lobes. They are sometimes quite deeply bifid or may be truncate and obtuse, but they are always sparsely 'pubescent' with small hair-like papillae, and have no dorsal ridge at all.

The small, uniformly coloured, rugulose and not very hairy corolla of *S. rufa* suggests a relationship with *S. kwebensis*, while the hairy corona suggests an affinity with *S. arenosa* and *S. rubiginosa*.

History

Stapelia rufa was discovered by Francis Masson on the western edge of the Little Karoo 'in hot places beyond Platteklouf, in other words in arid areas north of the present-day Gysmanshoek Pass. It flowered in his garden in Cape Town in 1793.

The var. *attenuata* described by N.E. Brown was discovered by N.S. Pillans in November 1904.

2. *Stapelia similis*

Stapelia similis N.E.Br., *Bull. Misc. Inform.* 1911: 358(1911).

Gonostemon similis (N.E.Br.) P.V.Heath, *Calyx* 1:19 (1992).

Type: South Africa, Richtersveld, in ravine near Doornpoort, H.H.W. Pearson 6134 (K).

Stapelia juttiae Dinter, *Neue Pflanzen Deutsch-SWAs:* 53, t. 60 (1914).

Gonostemon similis var. *juttiae* (Dinter) P.V.Heath, *Calyx* 3: 9 (1993).

Lectotype (selected here): Kanus, *Engler sub Dinter* 3252 (SAM).

Stapelia portae-taurinae Dinter & A.Berger, *Bot. Jahrb. Syst.* 50, Suppl.: 592 (1914).

Gonostemon similis var. *portae-taurinae* (Dinter & A.Berger) P.V.Heath, *Calyx* 3: 9 (1993).

Type: Namibia, Bullsport, Dinter 2596 (SAM).

Stapelia noachabibensis C.A.Luckh., *S.A.G.* '28: 228 (1938).

Type: Namibia, Noachebib, E. Rusch sub Lückhoff 257 (missing).

Lectotype (selected here): 'S.A.G.' '28: fig.

Small succulent forming dense clump mostly < 150 mm diam. but occasionally reaching 1 m diam., with many short slender stems. **Stems** 20-120 (-150) mm long, 5-12 mm thick, erect, shortly pubescent, pale green usually with purple in grooves between angles; **tubercles** 1-2 mm long, close together along stem, obscure and mostly barely distinguishable, joined into 4 obtuse angles along stem with slight grooves between angles (stem $\pm$ square in cross-section); **leaf-rudiments** 1.0-1.5 mm long. **Inflorescences** pubescent, usually 1 per stem near base, each with 1-6 flowers opening in gradual succession on short stout peduncle up to 20 mm long with deltoid bracts < 1 mm long; **pedicel** 30-80 mm long, 1.5-2.5 mm thick, brownish, spreading with upturned apex holding flower facing upwards $\pm$ on ground; **sepals** 3-4 mm long, 1.0-1.5 mm broad at base, ovate-lanceolate, acute, green. **Corolla** 15-28 mm diam., rotate to shallowly campanulate; outside green usually with 1-3 prominent (not raised) veins on each lobe; inside densely and coarsely transversely rugulose, yellow-brown to dark brown or almost black, glabrous, often with sweat-like droplets of nectar below bases of lobes; **tube** 1.5-4.0 mm long, $\pm$ 6 mm broad, cupular and steep-sided around gynostegium, with flat part of corolla often noticeably thickened into slight annulus around its mouth; **lobes** 6-10 mm long, 5-6 mm broad, spreading, ovate-deltate, acute to shortly acuminate, convex above from revolute ciliate margins. **Corona** $\pm$ 3 mm tall, $\pm$ 3-5 mm broad, raised on obtusely pentagonal stipe < 1 mm long, red-brown to black becoming red or yellow towards base, glabrous; **outer lobes** $\pm$ 1 mm long, 2 mm broad, spreading below middle of tube, $\pm$ rectangular, truncate to rounded, somewhat channelled on upper surface towards base, covered with fine sweat-like droplets of nectar; **inner lobes** 1.0-1.5 mm long, adpressed to backs of anthers and $\pm$ equalling them, dorsiventrally flattened, deltoid, acute, sometimes with slight dorsal swelling near base.

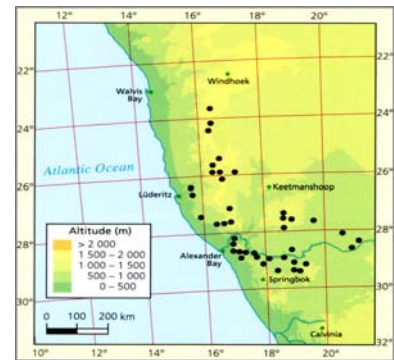


Fig. 15.9. Distribution of *Stapelia similis*.

Distribution and habitat

Stapelia similis is widely distributed in the southern part of Namibia and in Namaqualand and Bushmanland of South Africa. In Namibia it is mainly found along the eastern margin of the Namib from south-west of Rehoboth to Witpiitz. Records have also been made on many of the isolated hills and mountains in the southern part of the desert from Sturmhaube southwards to the Aurus Mountains. This area receives winter-rainfall. The species also occurs around the southern and western edge of the Great Karas Mountains and in the Warmbad district. In South Africa it is particularly well known from the Richtersveld but it is also recorded eastwards along the Orange River to Upington. Giess (1982) mentioned material that he had seen from the Brandberg in central Namibia but it is probable that this referred to the small- and dark-flowered plants discussed below under *S. kwebensis*.

Stapelia similis is mostly found in extremely arid habitats. In the arid south plants grow on stony slopes and shelter between rocks or under small bushes, only rarely occurring on stony flats. Further north, between Helmeringhausen and Rehoboth, it grows mainly on gravelly flats, often sheltering under shrubs of the *driedoring*, *Rhigozum trichotomum*. The rocks among which it grows may be granite, schist or dolomite and in South Africa it may also be encountered on low hills covered by quartz gravel.

Diagnostic features and relationships

In *S. similis* the stems are neatly and tightly packed into clumps which are mostly small but occasionally reach 1 m in diameter. In such cases the clump consists of vast numbers of stems and is probably quite old. The stems are invariably quite distinctive and are slender,

STAPELIA SIMILIS



Fig. 15.10. *S. similis*, PVB 5674, south-west of Maltahöhe, Namibia, in habitat, March 1993.



Fig. 15.11. *S. similis*, PVB 5227, just north of Pofadder.



Fig. 15.12. *S. similis*, PVB 3490, north-west of Upington.

erect and pale green with a darker colour in the slight grooves between the angles. The tubercles are quite close together along the stems and are small and inconspicuous, if visible at all. These stems are indistinguishable in shape and colour from those of *S. olivacea* and *S. pearsonii*.

Flowers are borne on comparatively long pedicels which usually spread away from the plant to place the flower facing upwards on the ground, though they can be ascending on occasion. If good rains have been received, plants may be surrounded by a ring of flowers on the ground. They are fairly small (mostly around 20 mm across), dark brown and are heavily rugulose inside. In the centre of the flower there is a small cupular tube, the mouth of which may be emphasised by a distinct annular thickening.

The corona in *S. similis* is small and contained within the corolla tube. It has very short outer lobes, which are generally much shorter than broad, and these spread out to touch the side of the tube. The little inner lobes are adpressed to the anthers and more or less equal them. The outer corona lobes are usually dotted with small quantities of nectar and little pools of this also accumulate between the ridges on the

corolla in the tube and around its mouth. These attractants are supplemented by a fairly strong, excrement-like odour.

The distribution of *S. similis* is generally a little to the south-west of that of the very widely ranging *S. kwebensis*, although the two distributions overlap in a broad band running north-west to south-east from the Naukluft through Maltahöhe, around Bethanie and on to the southern parts of the Great Karas Mountains. For both species this region of overlap is on the edge of their distribution and in localities in these areas both of them are quite rare. Leach (1985: 105) stated that it was 'in the northern areas of its distribution that *S. similis* is most variable and tends to merge with ... *S. longipedicellata*'. I have seen no evidence for this statement in any of several localities where I have seen both species. The fact that they are clearly distinguishable over the whole of this common area indicates that, despite the differences between them not being very large (so they are clearly closely related), they are distinct biological species. The differences between the two lie in the longer leaf-rudiments of *S. kwebensis* and the longer, prostrate pedicel of *S. similis*.

Stapelia similis is also close to the southern Angolan endemic *S. parvula*. The latter differs mainly in having shorter stems (which seldom exceed a length of 30 mm, according to Leach (1985)); the much smaller flowers (up to 7.5 mm in diameter whereas they are at least 15 mm across in *S. similis*); and the fact that the corona is not included in the tube, which is always the case in *S. similis*.

History

Early collections of *S. similis* seem to have been made by several people at much the same time. Jutta Dinter, while botanising near Aus in Namibia together with her husband M. Kurt Dinter, collected material in December 1910 that was described by Kurt Dinter in 1914 as *Stapelia juttae*. Pearson collected the material from which *S. similis* was described near Doornpoort in the Richtersveld on 1 January 1911, during the Percy Sladen Memorial Expedition of 1910-11 to the Orange River, and N.E. Brown named it in 1911. H.G. Adolf Engler also gathered it south of the Great Karas Mountains in April 1913 while on a collecting trip with Dinter.

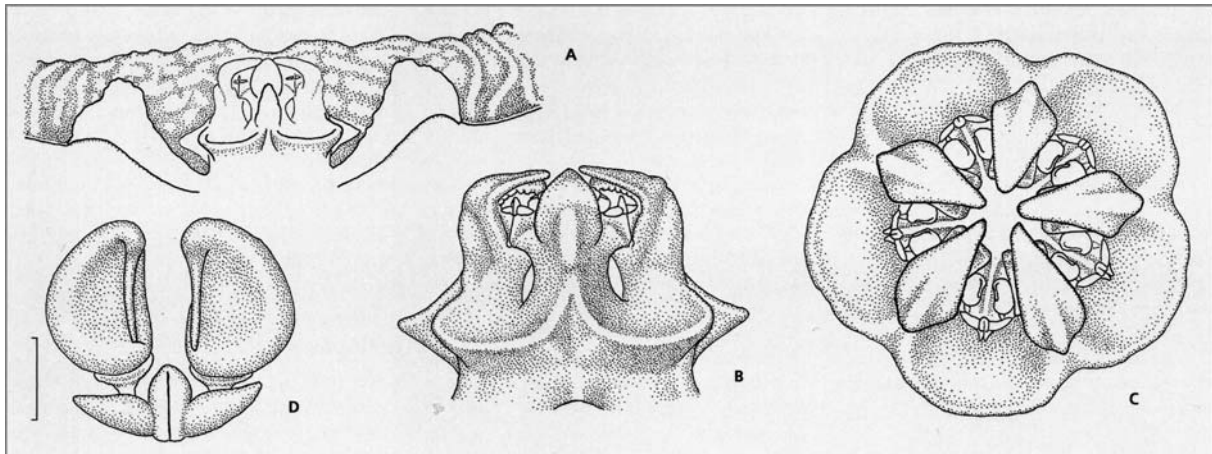


Fig. 15.13. *Stapelia similis*. A, side view of dissected flower. B, side view of gynostegium. C, face view of gynostegium. D, pollinarium. Scale bars: A, 3 mm (at D); B, C, 1 mm (at D); D, 0.25 mm. Drawn from A, B, D, PVB 7199, east of Witpiitz, Namibia; C, *Aslander*, east of Springbok.



Fig. 15.14. *S. simile*, PVB 5653, Bullsport, at the base of the Naukluft, Namibia, in habitat, March 1993.

3. *Stapelia kwebensis*

Stapelia kwebensis N.E.Br., *Fl. Trop. Afr.* 4 (1): 501 (1903).

Gonostemon kwebensis (N.E.Br.) P.V.Heath, *Calyx* 1: 19 (1992).

Lectotype: Botswana, Kwebe Hills, C.E. Lugard 29 (K).

Stapelia kwebensis var. *longipedicellata* A.Berger, *Stap. u. Klein.*: 318 (1910).

Stapelia longipedicellata (A.Berger) N.E.Br., *Bull. Misc. Inform.* 1913: 303 (1913).

Gonostemon longipedicellatus (A.Berger) P.V.Heath, *Calyx* 1:19 (1992).

Lectotype (selected here): Namibia, near Olukonda, Sept. 1885, Schinz (Z).

Small succulent forming compact to diffuse clump 50-500 mm diam. **Stems** 60-200 mm long, 8-15 mm thick, erect to spreading, shortly pubescent, grey-green with darker green to purple in grooves between angles; **tubercles** 2-3 mm long, widely spaced along stem, obscure, joined into 4 obtuse angles along stem with stem distinctly concave between angles; **leaf-rudiments** 2-7 mm long, lanceolate, acute. **Inflorescences** pubescent, 1-3 per stem arising at any height on stem, each with 1-6 flowers developing in gradual succession on stout spreading to erect peduncle 5-10 mm long, with deltoid bracts up to 1 mm long; **pedicel** 10-50 mm long, 1.5 mm thick, pale green to purplish, ascending to spreading and often holding flower facing upwards; **sepals** 3.5-5.5 mm long, 1-2 mm broad at base, ovate, acuminate. **Corolla** 15-45 mm diam., rotate to slightly campanulate; outside purplish to pale green; inside usually transversely rugulose over most of surface with rugosities fading to absent in tube, sometimes only very faintly transversely rugulose on lobes, purple- to red- to yellow-brown (or greenish) on lobes sometimes changing to red around mouth of tube and sometimes paler in tube (rarely altogether almost black), glabrous but finely papillate; **tube** 3-5 mm long, $\pm$ 5 mm broad, shallowly bowl-shaped to cupular, rarely slightly pentagonal, with corolla often noticeably thickened around mouth; **lobes** 5-15 mm long, 7-9 mm broad at base, spreading to slightly reflexed, ovate, acuminate, convex with margins reflexed. **Corona** $\pm$ 2.5-3.5 mm tall, $\pm$ 3.5 mm broad, purple-red to red, raised on very short stipe $<$ 0.5 mm long, glabrous; **outer lobes** $\pm$ 0.5 mm long, 1.0-1.5 mm broad, spreading, $\pm$ rectangular, truncate to sometimes subacute; **inner lobes** 0.50-0.75 mm long, adpressed to backs of anthers and sometimes slightly exceeding them, dorsiventrally flattened, deltoid to lanceolate, acute, slightly swollen dorsally at base.

Distribution and habitat

Stapelia kwebensis has the broadest distribution in an east-west direction of any species of *Stapelia*. In Namibia it is distributed widely and has been recorded from the northern parts of the Kaokoveld to the Great Karas Mountains in the south, generally east of the Namib and west of the Kalahari. In Botswana it is found particularly in the calcareous areas of the Mkari-kari and other pans in the centre but also occurs

STAPELIA KWEBENSIS

westwards towards the border with Namibia and eastwards towards the valley of the Limpopo River in Zimbabwe and the northernmost part of South Africa. It is found further east in Zimbabwe in the Sabi River valley and has been collected near Pafuri in Mocambique.

Plants are mostly found in flat, stony areas and are frequently seen on calcrete. Larger specimens often grow in the open among stones but equally often they grow inside a bush (frequently small shrubs of *Acacia tortilis*). *Stapelia kwebensis* is often associated with *Colophospermum mopane* - in fact, its distribution to a large extent coincides with the drier parts of the distribution of *C. mopane*. It becomes especially common in overgrazed patches around villages, generally occurring in such spots with several other stapeliads. In the Limpopo Valley it is one of several stapeliads occurring socially with *S. gettliffei*, while in Namibia it frequently grows with *Duvalia polita*, *Huernia oculata* and *S. schinzii*.

Diagnostic features and relationships

Plants of *S. kwebensis* have the stems grouped into quite dense, shrub-like clumps. In the field, these shrublets are mostly rooted in the centre with the side-branches produced above the

ground and only rarely rooting (though they root readily as cuttings). The central stems in a clump are erect and those on the sides tend often to spread. Specimens do not have the spreading habit found in other species such as *S. gettliffei*. Whereas most of the tropical stapeliads are thick-stemmed, *S. kwebensis* has slender stems which are pale green with a darker area between the angles, though this is not generally as dark as in *S. olivacea*.

Flowers in *S. kwebensis* are less variable in size than one might expect over so large a range and are usually about 30 mm in diameter. Mostly they are more or less flat, with a small, bowl-shaped tube containing the corona in the centre. This tube often has a slightly thickened ring of tissue around its mouth. In and around the base of the Brandberg of Namibia some plants are known with much smaller flowers (about 20 mm in diameter) with a conspicuous, cupular tube about as deep as broad (fig. 15.17, see also Bruyns 1990b). Here, as in Leach (1985), these are considered to belong to *S. kwebensis* (rather than to *S. similis*), since the flowers are held on ascending pedicels. Generally in *S. kwebensis* the colour of the inside of the flowers varies from yellowish to greenish brown to dark red-brown and sometimes the tube is paler than the rest but it may even be slightly darker. In plants from the Brandberg the flower may be nearly

black inside. All specimens I have encountered have had very evil-smelling flowers which emit an excrement-like odour.



Fig. 15.15. *S. kwebensis*, PVB 6515, east of Makalambedi, Botswana.

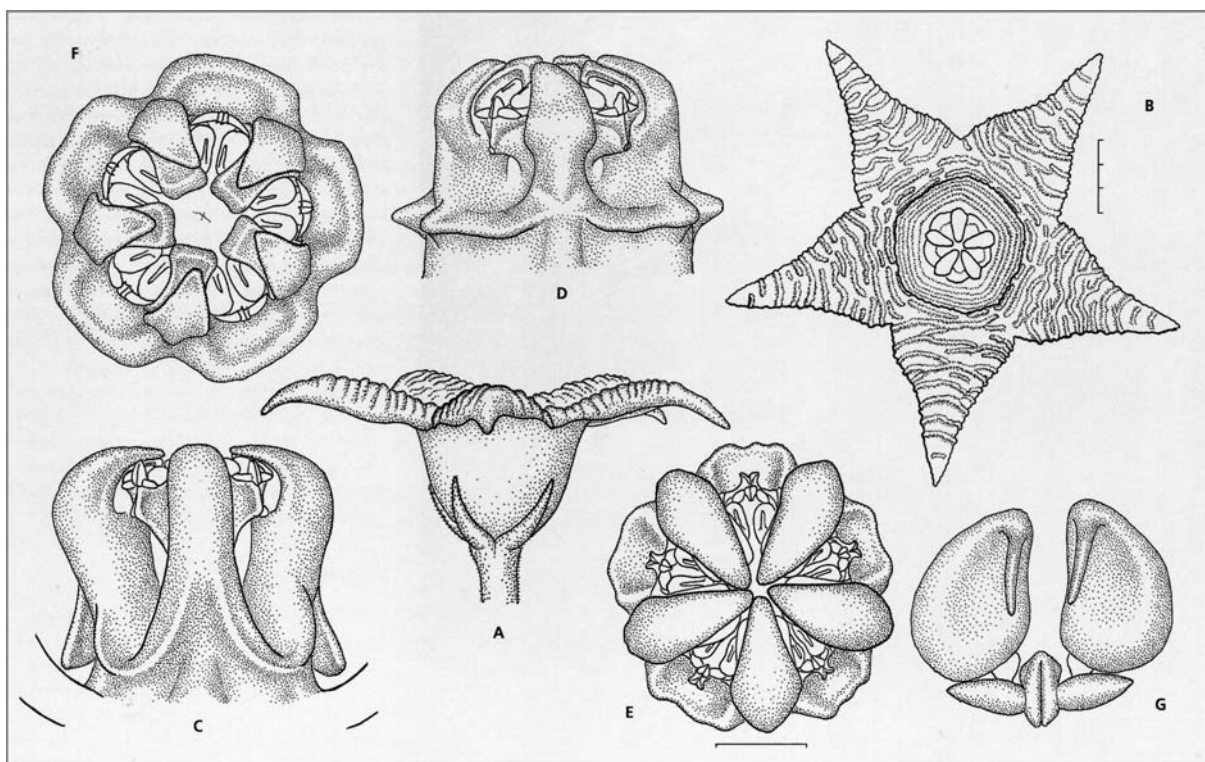


Fig. 15.16. *Stapelia kwebensis*. A, side view of flower. B, face view of flower. C, D, side view of gynostegium. E, F, face view of gynostegium. G, pollinarium. Scale bars: A, B, 3 mm (at B); C-F, 1 mm (at E); G, 0.25 mm (at B). Drawn from A, B, C, E, PVB 2355, Goaseb Schlucht, Brandberg, Namibia; D, F, PVB 3574, near Aroab, Namibia.

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As in *S. similis*, the corona in *S. kwebensis* consists of extremely short outer lobes which are about half as long as broad. Beneath the guide-rail there is an upward-pointing lip behind which lies a considerable 'nectarial cavity' (fig. 30 B). The gynostegium is also unusually tall but has very short inner lobes which are pressed to the backs of the anthers.

Leach (1985) recognised two very closely related 'species': *S. kwebensis* and *S. longipedicellata*. The latter was found in Namibia and the former mainly in Botswana and eastwards, but also in northern Namibia and crossing over the distribution of *S. longipedicellata* to appear again in the Kaokoveld. He mentioned that *S. longipedicellata* is 'by far the most variable member of the closely related group which includes *S. kwebensis*, *S. similis* and *S. parvula*' (p. 103). From *S. kwebensis* it differs by the 'somewhat smaller leaves which have a greater tendency to become white and marcescent' and the quite different inflorescences 'with a stout relatively long, erect peduncle and long, erect pedicels bearing flowers ... facing upwards'.

It is my experience that the leaves generally become longer in areas of higher rainfall and consequently they are shortest in the localities to the west, which are mainly occupied by *S. longipedicellata*. As far as the inflorescence is concerned, some very stout, erect peduncles are found on some plants of *S. kwebensis*, whereas some plants with long pedicels have almost no peduncle at all. This is particularly the

case in northern Namibia (where a transition between the two species might be expected, if such existed), and in this area the flowers are held facing upwards or outwards. I have been unable to find any difference in the pedicels which seem, generally, to become shorter as one progresses eastwards. Therefore, there do not seem to be any grounds for the recognition of two distinct species.

Leach also mentioned (p. 103) that where the distributions of *S. longipedicellata* and *S. similis* are close, the respective sizes of the flowers and the pollinia approach one another. Plants of *S. similis* have been collected within 1 km of those of *S. longipedicellata* (e.g. in the Great Karas Mountains north of Grünau and also north and west of Maltahöhe) and there has been no sign of any intergradation



Fig. 15.17. *S. kwebensis*, PVB 2824, Basswaldrinne, Brandberg, Namibia. The long pedicels and small, cupular flowers suggest that this may be a northern outlier of *S. similis* but here it is considered to belong to *S. kwebensis*.

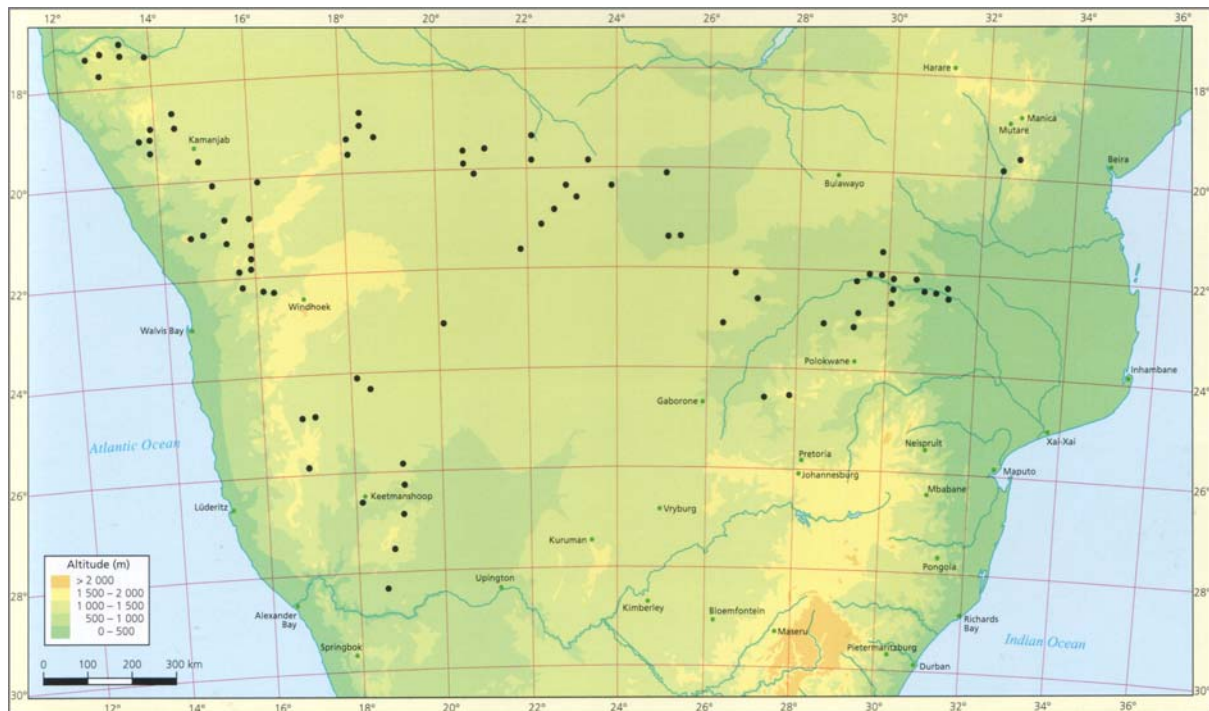


Fig. 15.18. Distribution of *Stapelia kwebensis*.

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between the two. The fact that these two taxa co-exist over a wide area without either intergradation or even any apparent hybrids being formed suggests that two distinct species are involved and, while *S. similis* and *S. kwebensis* are very closely allied, there are no grounds for claiming that *S. longipedicellata* 'appears to be rather more closely related to *S. similis* than to *S. kwebensis*'.

History

Stapelia kwebensis was discovered in January 1897 by Edward J. Lugard and his wife Charlotte Eleanor in the Kwebe Hills, which lie to the south-west of Maun, in northern Botswana. Material described as *S. kwebensis* var. *longipedicellata* was actually collected earlier. These plants were gathered by Hans Schinz in September 1885, around the mission station at Olukonda in Ovamboland in northern Namibia.



Fig. 15.19. *S. kwebensis*, PVB 3574, near Aroab, Namibia.



Fig. 15.20. *S. kwebensis*, PVB 6433, south of Shoshong, Botswana.



Fig. 15.21. *S. kwebensis*, PVB 5714, west of Helmeringhausen, Namibia.

4. *Stapelia olivacea*

Stapelia olivacea N.E.Br., Gard. Chron. N.S. 3:136 (1875).

Gonostemon olivaceus (N.E.Br.) P.V.Heath, *Calyx* 1:19 (1992).

Type: South Africa, Cape, comm. J. Shaw (K).

Small succulent forming compact clump 50-150 mm diam. **Stems** 20-120 mm long, 6-10 mm thick, erect, shortly pubescent, grey-green, with purplish flecks and darker green in grooves between angles; **tubercles** 1-2 mm long, obscure, joined into 4 obtuse angles along stem with stem slightly concave between angles; **leaf-rudiments** 1.0-1.5 mm long. **Inflorescence** pubescent, 1 per stem arising near base, with 1-6 flowers developing in gradual succession on short stout peduncle < 10 mm long, with deltoid bracts up to 1 mm long; **pedicel** 4-6 mm long, 1.5 mm thick, pinkish, ascending to spreading and holding flower facing outwards; **sepals** ovate-lanceolate, acute, 4-5 mm long, 1.5 mm broad at base. **Corolla** 20-40 mm diam, $\pm$ rotate to slightly campanulate, lobed to about middle of radius; outside purplish to greenish, with 3 darker veins on each lobe; inside transversely rugulose over whole surface, mostly almost black but sometimes red-brown to yellow-brown (olive-green), glabrous; **tube** 2-4 mm long, 4-6 mm broad, $\pm$ bowl-shaped, pentagonal with radiating grooves in corolla below sinuses of lobes; **lobes** 7-15 mm long, 6-8 mm broad at base, spreading, ovate-deltate to ovate-lanceolate, acute, $\pm$ flat above or with margins slightly recurved, often with dense row of fine white hairs along margins. **Corona** $\pm$ 1 mm tall, $\pm$ 7 mm broad, purple-black to red, raised on very short obtusely pentagonal stipe < 1 mm long, glabrous; **outer lobes** 2.5-3.5 mm long, 1 mm broad, spreading onto surface of corolla, narrowly deltoid, obtuse to truncate, slightly channelled above; **inner lobes** 4-5 mm long, adpressed to backs of anthers then erect and recurved above, dorsiventrally flattened towards base becoming slender and $\pm$ terete above, with slender ($\pm$ as broad as thick) acuminate ascending-spreading and laterally flattened dorsal wing.

Distribution and habitat

Stapelia olivacea is widely but scantily recorded over much of the Great Karoo but seems to be entirely absent from Bushmanland. It is mainly found in the former Cape Province of South Africa, with a single collection from the western Free State. Records exist from near Olifantshoek southwards to Fraserburg and eastwards to Colesberg and Cradock. There is a single, somewhat doubtful record from near Warmbad in Namibia which has been left off the distribution map.

This species is particularly associated with dolerite hills and dolerite-capped, shale mountains. Usually plants are found quite high up on these mountains and they grow among stones or boulders alongside or in small tufts of grass or shrublets.

Diagnostic features and relationships

Plants of *S. olivacea* always form tight, neat clumps of stems that are usually not more than 100 mm in diameter. The stems are fairly slender, with very obscure tubercles and they are greyish along the angles with dark green to purple in the grooves between the angles. Consequently they are essentially bicoloured, the two colours forming slender, vertical strips. This might be an adaptation for concealment among clumps of grass.

Flowers of *S. olivacea* are relatively small and often nearly flat, with fairly short, ovate lobes. They generally have a fringe of fine, white hairs along the margins and the inner surface is fairly densely and coarsely, transversely rugulose but glabrous. In colour they are relatively variable. Many of them in the

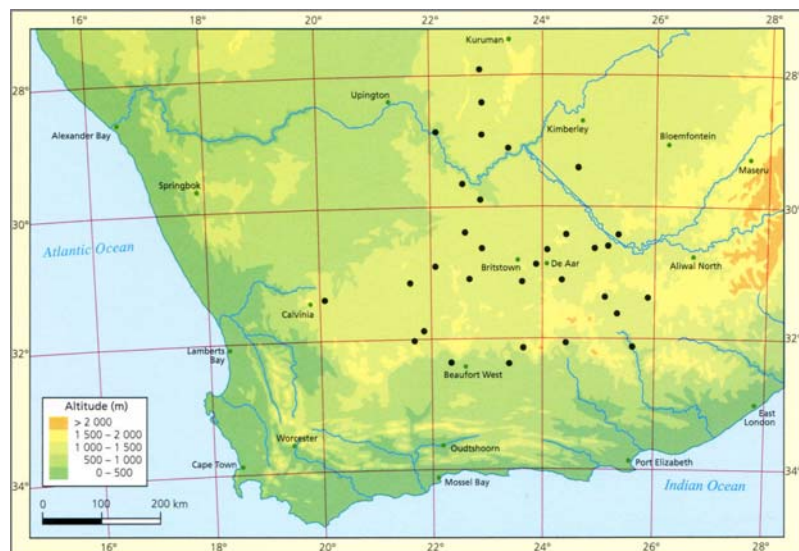


Fig. 15.22. Distribution of *Stapelia olivacea*.



Fig. 15.23. *S. olivacea*, PVB 7790, west of Colesberg.



Fig. 15.24. *S. olivacea*, PVB 4506, west of Griquatstad, plant with unusually small flowers.



Fig. 15.25. *S. olivacea*, PVB 4536, near Douglas. In this area the flowers lack the conspicuous fringe of white marginal hairs on the lobes.

Great Karoo are dark and almost black inside. In contrast to this, the original plant described by N.E. Brown (which was of unknown origin) had olive-green flowers with brown rugosities. According to A. Berger (1910), the olive-green colour of the painting that appeared in the *Botanical Magazine* (Thistleton-Dyer 1876) is wrong, but a recent collection from around Colesberg (PVB 7790) has exactly the coloration described by Brown and figured in the *Botanical Magazine*. Plants from Douglas to Griquatstad have proved to have paler flowers, which vary from brown to nearly orange. In these plants the corolla has longer and narrower lobes and the lobes are without marginal hairs, as mentioned by White & Sloane (1937: 523).

The flowers usually emit a strong, offensive odour of excrement but greenish ones have a mushroom-like smell which is not that unpleasant.

The red to nearly black corona has slender and fairly long lobes in both the inner and outer series.

Stapelia olivacea and *S. pearsonii* are very closely allied indeed. Leach (1985) also mentions a relationship with *S. flavopurpurea* but that species appears to be altogether more



Fig. 15.26. *S. olivacea*, Bouwer, Graaff-Reinet.

distantly related. *Stapelia flavopurpurea* differs from both of them by the dense patch of clavate hairs below the bases of the lobes, the peculiar colouring of the inside of the corolla, the differently shaped outer corona lobes and the unusually narrow pollinia. Therefore, while the coronas and pollinaria of *S. olivacea* and *S. pearsonii* are almost identical, the same is not true of *S. olivacea* and *S. flavopurpurea*.

History

Stapelia olivacea was described from plants sent in April 1874 to N.E. Brown and also from some which were cultivated at Kew. These specimens were sent by John Shaw, who was then living in Cape Town, but it is not known where they were collected. There do not seem to be any earlier records of this species.

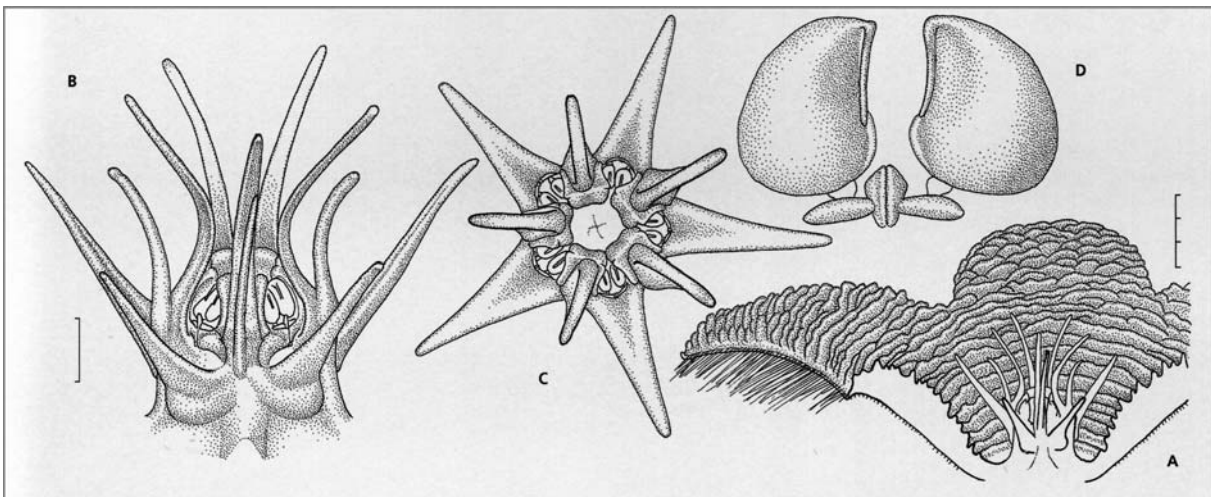


Fig. 15.27. *Stapelia olivacea*. A, side view of dissected flower. B, side view of gynostegium. C, face view of gynostegium. D, pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at B); D, 0.25 mm (at A). Drawn from Bouwer, Graaff-Reinet.

STAPELIA PEARSONII

5. *Stapelia pearsonii*

Stapelia pearsonii N.E.Br., *Bull. Misc. Inform.* 1913:304(1913).

Gonostemon pearsonii (N.E.Br.) P.V.Heath, *Calyx V.* 19 (1992).

Type: Namibia, Great Karasberg, *Pearson 8539* (BOL, holo.; PRE, iso.).

Small succulent forming compact clump 40-150 mm diam. **Stems** 20-80 (-120) mm long, 5-8 (-12) mm thick, erect, shortly pubescent, grey-green, with purplish flecks and darker green in grooves between angles; **tubercles** 1-2 mm long, obscure, joined into 4 obtuse angles along stem with stems $\pm$ square in cross-section; **leaf-rudiments** up to 1 mm long. **Inflorescence** pubescent, 1 per stem arising near base, with 1-6 flowers developing in gradual succession on short stout peduncle < 5 mm long with deltoid bracts up to 1 mm long; **pedicel** 30-40 mm long, 1.5 mm thick, pinkish, ascending and holding flower facing upwards; **sepals** 2.5-3.5 mm long, 0.5-1.0 mm broad at base, lanceolate, acute. **Corolla** 35-50 mm diam, rotate, deeply lobed; outside purplish to greenish, with 3 darker veins on each lobe; inside finely transversely rugulose becoming smooth in tube, sometimes with longitudinal groove on lobes, pale yellow-brown to deep red-brown, becoming paler towards centre, glabrous; **tube** 1-3 mm long, 4-6 mm broad, $\pm$ bowl-shaped, pentagonal with corolla somewhat swollen below bases of lobes and with radiating grooves below sinuses of lobes; **lobes** 12-15 mm long, 8 mm broad at base, spreading, narrowly ovate, acute, convex above from revolute margins, without cilia. **Corona** $\pm$ 6 mm tall, 8 mm broad, dark purple-brown to red and somewhat shiny, raised on obtusely pentagonal stipe 1-2 mm long, glabrous; **outer lobes** 3-4 mm long, 1 mm broad, spreading onto surface of corolla, narrowly deltoid, obtuse, very slightly channelled towards base (otherwise flat above); **inner lobes** 3-4 mm long, adpressed to backs of anthers then connivent-erect in column above style apex and recurved above, dorsiventrally flattened

towards base becoming slender terete above, with slender ($\pm$ as broad as thick) acuminate spreading laterally flattened dorsal wing near base.

Distribution and habitat

Stapelia pearsonii is only known from the Great Karas Mountains in southern Namibia and so is one of the most localised species of *Stapelia*. It is quite widespread on the mountains and has been seen on their eastern, western and northern flanks. Plants are usually very scattered but in one spot over 10 specimens were seen, so they may be locally fairly common.

Specimens of *S. pearsonii* grow in rocky places, usually on granite. They have been located from near the base of the mountains at about 1 300 m to around 1 600 m but were even found on schist's at about 2 000 m on one of the highest peaks, in the so-called *Schroffenstein*.

Diagnostic features and relationships

Plants of *S. pearsonii* form particularly neat clusters of erect, slender stems that are packed quite closely together into a clump.

The inside of the flower in this species is very variable in colour, ranging from dark red-brown to quite pale yellow-brown. The flowers always seem to become paler towards the centre. A foetid, urine-like odour is emitted. The lobes often spread quite strongly so that the fused area around their bases is pushed forward somewhat like a small annulus. Another odd feature is that quite conspicuous grooves run down into the tube from the bases of the lobes and the corolla is somewhat paler in these grooves. Between these grooves, the corolla is thickened below the lobes, accentuating the

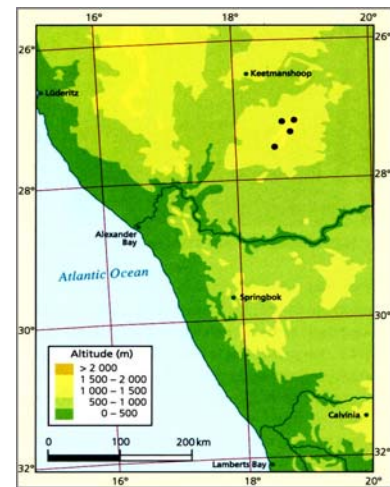


Fig. 15.28. Distribution of *Stapelia pearsonii*.

pentagonal shape of the tube. The stipe on which the corona sits, fits quite closely into this pentagonal base of the tube.

Stapelia pearsonii is very similar to *S. olivacea*, the stems of the two species being more or less identical in size, shape and colouring. Their respective coronas are also very similar, though the outer lobes are more deeply grooved above in *S. pearsonii*. The two differ in several other features. One is the longer pedicel in *S. pearsonii*, which holds the flower well away from the plant. Also in *S. pearsonii*, the inside of the flower is considerably more finely rugulose and these rugosities disappear in the tube. In addition, the flower is far more

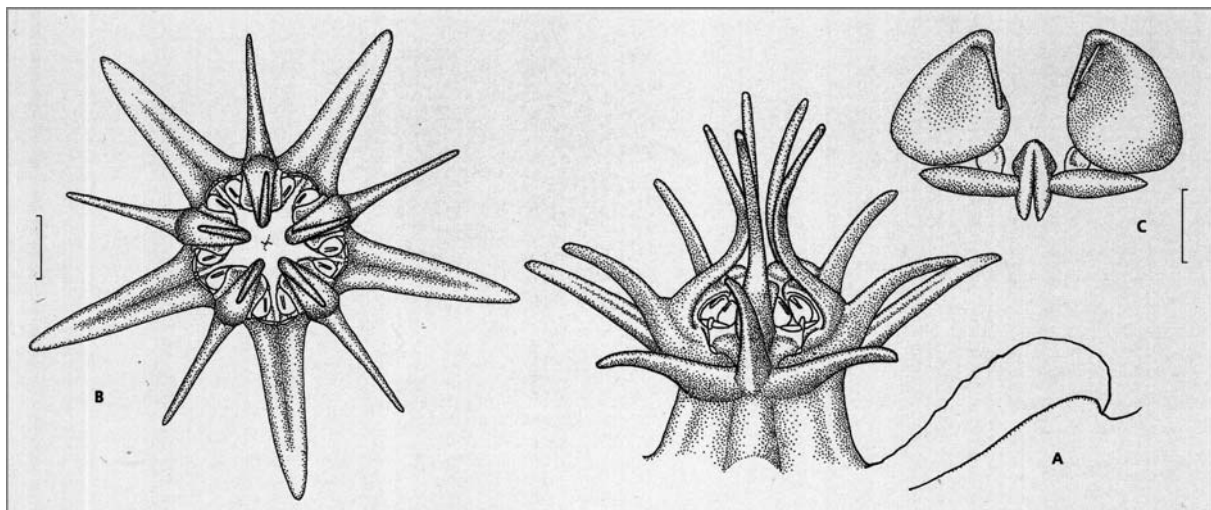


Fig. 15.29. *Stapelia pearsonii*. A, side view of gynostegium. B, face view of gynostegium. C, pollinarium. Scale bars: A-B, 1 mm (at B); C, 0.25 mm. Drawn from PVB 3531, eastern Great Karas Mountains, Namibia.

STAPELIA DIVARICATA

deeply lobed and has the margins of the lobes strongly folded back, without any cilia. This would make *S. pearsonii* easy to separate from 'typical' *S. olivacea* (as in fig. 15.23, 15.26), with its dark flowers with flat, short lobes fringed with white hairs. However, *S. olivacea* is more variable than previously thought and its flowers can also have somewhat longer, narrower lobes with reflexed, eciliate margins (e.g. fig. 15.25). These plants begin to resemble *S. pearsonii* considerably more and show that several of the distinctions given by Leach (1985) do not hold.

History

Stapelia pearsonii was first collected by Harold H.W. Pearson on rocks above the camel-path across the Great Karas Mountains between December 1912 and January 1913. This was during one of the last expeditions to Angola, Namaqualand and Namibia funded by the Percy Sladen Memorial Trust and on this occasion the expedition crossed the Great Karas Mountains from Narudas Slid to Kraikluft (today Pieters-kloof), i.e. from near the south-eastern corner

to the north-western side. According to Bolus *et al.* (1914) the species was seen at least twice during this period. Pearson seems to have considered that his collections represented *S. olivacea* but N.E. Brown considered them to belong to a new species. It was only known from this collection until it was rediscovered by W. Giess & M.A.N. Müller in May 1972. My own collecting in the Great Karas Mountains has revealed that it occurs widely in these relatively unexplored and rugged mountains.



Fig. 15.30. *S. pearsonii*, PVB 5776, south-western end of the Great Karas Mountains, Namibia.



Fig. 15.31. *S. pearsonii*, PVB 5776, south-western end of the Great Karas Mountains, Namibia.



Fig. 15.32. *S. pearsonii*, PVB 3552, northern end of Great Karas Mountains, Namibia, in habitat, January 2000, with the plant, flowering profusely and partially hidden by dry grass.

6. *Stapelia divaricata*

Stapelia divaricata Masson, Stap. Nov.: 17, t. 22 (1797).

Gonostemon divaricatus (Masson) Haw., Syn. Pl. Succ.: 27 (1812).

Type: South Africa, Cape, Masson (missing).

Lectotype (designated here): Masson, Stap. Nov.: t. 22.

Stapelia pallida J.C.Wendl., Coll. Pl. 2: 39, t. 51 (1809).

Gonostemon pallidus (J.C.Wendl.) Sweet, Hort. Brit., ed. 1: 278 (1826).

Type: none located in Wendland Herbarium (GOET).

Lectotype (designated here): J.C. Wendl., Coll. Pl. 2t. 51.

Stapelia stricta Sims, Bot. Mag. 46: t. 2037 (1819).

Gonostemon strictus (Sims) Haw., Suppl. Pl. Succ.: 12 (1819).

Lectotype: Bot. Mag. 46: t. 2037.

Stapelia pallens Steud., Nomencl. Bot., ed. 2, 2: 631 (1841).

Type: unknown.

Small succulent forming dense clump of closely packed stems, 60-300 mm diam. **Stems** 40-130 (-300) mm long, 4-12 mm thick, erect, $\pm$ glabrous, bright green tinged with purple towards tips; **tubercles** 1-2 mm long gradually becoming less prominent with age, fused into 4 obtuse angles along stem; **leaf-rudiments** 1-2 mm long. **Inflorescences** finely pubescent, 1-2 per stem, each of 1-10 flowers developing in close succession near base of stems from short peduncle with deltoid bracts 1-2 mm long; **pedicel** 12-20 mm long, 2 mm thick, spreading, often with upturned apex; **sepals** 4-5 mm long, 2 mm broad at base, ovate, acute. **Corolla** 40-55 mm diam., rotate or somewhat convex with reflexed lobes; outside creamy pink with 5 darker veins on each lobe; inside smooth and shiny to faintly rugulose towards centre, pale yellow or orange to pale purple or pale pink becoming paler towards centre, often with faint concentric broken transverse yellow lines towards and below bases of lobes, glabrous except in tube and on margins of lobes; **tube** $\pm$ 1.5 mm long, 4 mm broad, closely containing stipe of gynostegium, pentagonal, with mouth somewhat closed by inward-projecting slightly annulus-like thickening of corolla, pubescent towards base; **lobes** 15-18 mm long, 7-8 mm broad at base, spreading to reflexed, ovate-acuminate, convex above from revolute margins with straight white cilia up to 2.5 mm long. **Corona** $\pm$ 4 mm tall, $\pm$ 7 mm broad, raised on pentagonal stipe $\pm$ 1 mm long, glabrous; **outer lobes** 2-3 mm long, 1.5-2.0 mm



Fig. 15.33. Distribution of *Stapelia divaricata*.

STAPELIA DIVARICATA

broad, oblong, widening gradually to obtuse emarginate apex, lightly concave above, spreading-recurved, orange or yellow towards base changing to pale purple towards apex; **inner lobes** ± 1 mm long, adpressed to backs of anthers and slightly exceeding them, dorsiventrally flattened except for dorsal keel becoming more prominent towards base, ovate, acute, orange-brown.

Distribution and habitat

Stapelia divaricata is a very rare species. At present it is known from two localities east of Swellendam, where it grows on steep, north-facing slopes. Specimens are usually tightly wedged between stones and small bushes on exposed shale outcrops with a few other succulents belonging to *Anacampseros*, *Ceropegia*, *Crassula* and *Delosperma* and short clumps of grass.

Diagnostic features and relationships

In *S. divaricata* plants form dense and quite large clumps up to 300 mm in diameter and so they seem to become very old. In most plants that have been seen in habitat and in others grown from seed the stems have always been short and strictly erect. One exception observed was a plant which was sheltered by a tree and had long stems (up to 300 mm long) which spread and trailed on the ground. This growth is similar to that on the plant depicted by Masson (1796-8) as well as on the figure which appeared in the *Botanical Magazine* (Sims 1807) which was based on a specimen cultivated by J. Walker of Stockwell Common, London. Therefore it is possible that these were all grown in such shady situations which led to their straggling growth, and this might also



Fig. 15.34. *S. divaricata*, PVB 7331, east of Swellendam.

explain Masson's otherwise rather odd name, the 'straggling *Stapelia*'.

The stems are a distinctive, bright green colour and are glabrous with a slightly sandpapery texture. They are usually 6-8 mm thick and so are fairly slender for the genus.

Instead of the usual flat, somewhat hairy and rugulose surface that many flowers of *Stapelia* have, here the corolla is convex, with the lobes and their edges somewhat reflexed. Furthermore, the whole interior is shiny and varies in colour from pale yellow to orange or pink, with the colouring usually most intense on the lobes and becoming paler around the corona. Towards the bases of the lobes and for some distance below them the surface is

marked with broken, transverse to more or less concentric yellow lines. These lie on the upper surface of faint, transverse rugulosities. Hairs are entirely absent from the face of the flower and are restricted to the tube around the base of the corona and along the margins of the lobes.

The corona in *S. divaricata* consists of relatively short outer lobes which spread close to the surface of the annulus and are orange around the base, becoming darker near their tips. The inner lobes are very short, just exceeding the anthers, and there is usually also a slight dorsal keel.

With its reflexed corolla lobes narrowed by their folded margins, the flower of *S. divaricata*

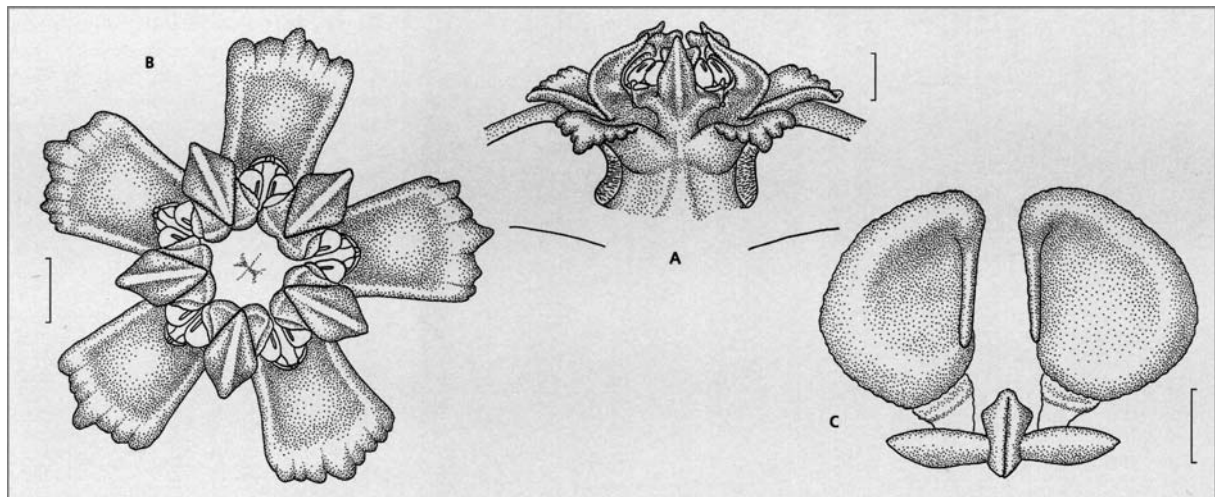


Fig. 15.35. *Stapelia divaricata*. A, side view of centre of dissected flower. B, face view of gynostegium. C, pollinarium. Scale bars: A, 1 mm; B, 1 mm; C, 0.25 mm. Drawn from PVB 1182, east of Swellendam.



Fig. 15.36. *S. divaricata*, PVB 7331, east of Swellendam. The flowers of this plant are somewhat similar to those of *S. cedrimontana* both in shape and in colouring.



Fig. 15.37. *S. divaricata*, PVB 7331, east of Swellendam.



Fig. 15.38. *S. divaricata*, PVB 1182, east of Swellendam.

looks somewhat like that of a strangely coloured form of *S. cedrimontana*. There is no doubt that the species' geographical situation and most of the features of its flower mean that it is closely related to the other species of the south-western Cape. The flower is, however, more shiny and smooth than that of any other species.

History

Stapelia divaricata was discovered by Francis Masson and flowered in his little garden at Cape Town in 1792. The next recorded collection was made by Kate C. Stanford in May 1935 near Heidelberg. Very few other collections have been made and it is almost certainly the rarest and most localised species of *Stapelia* known today.

7. *Stapelia glanduliflora*

Stapelia glanduliflora Masson, *Stap. Nov.*: 16, t. 19 (1797), as '*S. glandulifera*' in Willd., *Sp. PL* 1: 1284 (1798).

Gonostemon glanduliflorus (Masson) P.V.Heath, *Calyx* 1:19 (1992).

Type: South Africa, around North Olifants River, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t.19.

Stapelia hispidula Hornem., *Hort. Bot. Haft.* 1: 251 (1813) as '*S. hispida*' in Rust, *Monatsschr. Kakteenk.* 6: 37 (1896).

Lectotype (selected here): Cape of Good Hope, 'Hort. Haft. 1810' (C).

Stapelia glanduliflora var. *emarginata* N.E.Br., *Fl. Cap.* 4(1):968(1909).

Gonostemon glanduliflora var. *emarginatus* (N.E.Br.) P.V.Heath, *Calyx* 3: 9 (1993).

Lectotype: near Clanwilliam, Bishop, comm. Barkly (K).

Stapelia glanduliflora var. *haworthii* A.Berger, *Stap. u. Klein.*: 289 (1910).

Lectotype: Smith, *Exot. Bot.* 2: t. 71 (1805-08).

Stapelia glanduliflora var. *massonii* A.Berger, *Stap. u. Klein.*: 289 (1910).

Type: as for *S. glanduliflora*.

Small succulent forming compact clump 150-500 mm diam. **Stems** 30-150 mm long, 8-15 mm thick, erect, shortly pubescent, grey-green to purplish; **tubercles** 2-4 mm long, low and conical, joined into 4 obtuse angles along stem between which stem slightly concave; **leaf-rudiments** 1.5-2.0 mm long. **Inflorescence** pubescent, 1 per stem, of 1-10 flowers developing in close succession on stout peduncle up to 10 mm long with several deltoid bracts; **pedicel** 20-50 mm long, 1.5-2.0 mm thick, pinkish to green, spreading with upturned apex holding flower facing upwards $\pm$ on ground; **sepals** 3-4 mm long, 1 mm broad at base, lanceolate, acuminate, acute, green to brownish towards apices. **Corolla** 25-35 mm diam., rotate; outside cream-green with 3-5 darker impressed veins per lobe; inside faintly rugulose towards centre and smooth in upper half of lobes, pale yellow-green faintly transversely mottled with purple, becoming purple in tube, densely covered with translucent-white clavate hairs up to 3 mm long on lobes mainly towards margins (with bare patch along middle of each lobe) and on central

united portion of corolla to mouth of tube, with few fine small clavate hairs along margins and dense mat of small adpressed clavate hairs in tube (facing mouth); **tube** $\pm$ 2 mm deep, broadly bowl-shaped, with corolla thickened around mouth; **lobes** 12-15 mm long, 5-7 mm broad at base, spreading with tips usually somewhat reflexed, ovate-attenuate. **Corona** $\pm$ 5 mm tall, $\pm$ 7 mm broad, raised on obtusely pentagonal reddish stipe $\pm$ 1 mm long, glabrous; **outer lobes** $\pm$ 2 mm long, spreading, lanceolate with narrowly obtuse apex, yellow to orange towards base becoming purplish towards apex and along margins; **inner lobes** 2.0-2.5 mm long, reddish to purple, flecked with yellow, adpressed to backs of anthers then erect beyond them, dorsiventrally flattened below becoming terete above, subulate-attenuate, sometimes with slight dorsal ridge towards base.

Distribution and habitat

Stapelia glanduliflora is found mainly along the valley of the Olifants River from near Klawer to about 20 km north of Citrusdal.

Plants grow on stony slopes among shrubs of *Montinia caryophyllacea*, *Euphorbia mauritanica* and various other succulents which often include *E. loricata* as well as *Huernia guttata* and, occasionally, *Tromotriche revoluta*.

Diagnostic features and relationships

Stapelia glanduliflora produces its flowers on quite long pedicels which descend from the peduncle to the ground and then have an upturned apex so that the flower faces upwards more or less on the ground. A large specimen surrounded by flowers on the ground around it can make quite a show. The flowers are a little over 25 mm in diameter and seem to be odourless. Their most striking feature is the thick mat of whitish hairs that appear to cover them inside. These hairs are 2-3 mm long and distinctly clavate, with a slender base where they are attached to the surface. They are actually translucent, appearing white from a distance only and they remain filled with liquid while the flower is open. A closer examination of the flower shows that they do not arise uniformly over the whole surface. They are densely clustered on the flat, united area just below the lobes and on the lower half of the lobes but on the upper half they are mainly produced along the edges. Hairs are also present in the small tube around the base of the corona but these are tiny. The inner surface of the corolla is pale greenish yellow and transversely striped with pale red but these colours are largely obscured by the hairs.

Stapelia glanduliflora has a fairly small gynostegium with very short, deltoid outer lobes and almost filiform inner lobes. The whole structure is orange suffused with purple and nestles among the strange, translucent hairs on the corolla in a manner reminiscent of the

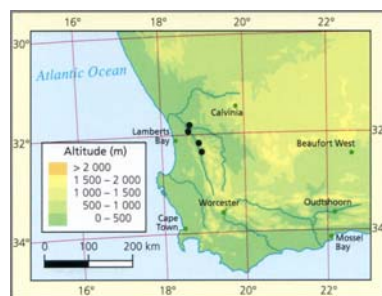


Fig. 15.39. Distribution of *Stapelia glanduliflora*.

STAPELIA GLANDULIFLORA

way that small fishes sometimes hide among the tentacles of a sea anemone.

This species is closely related to *S. erectiflora* and the differences between them are discussed under that species.

History

Stapelia glanduliflora was discovered by Francis Masson in 'dry areas around North Olifants River' and flowered at Kew in 1796. The figure that he made of it is not obviously identifiable with what is at present called *S. glanduliflora*, which was illustrated very clearly in Phillips (1932b). In Masson's plant the flower is held well above the ground on quite a short pedicel. However, it is densely covered inside with very obviously glistening, clavate hairs so his figure must be of what we know today as *S. glanduliflora*.



Fig. 15.40. *S. glanduliflora*, PVB 570, north of Citrusdal along Olifants River, in habitat, July 2004.



Fig. 15.41. *S. glanduliflora*, PVB 570, north of Citrusdal along Olifants River, in habitat, July 2004.

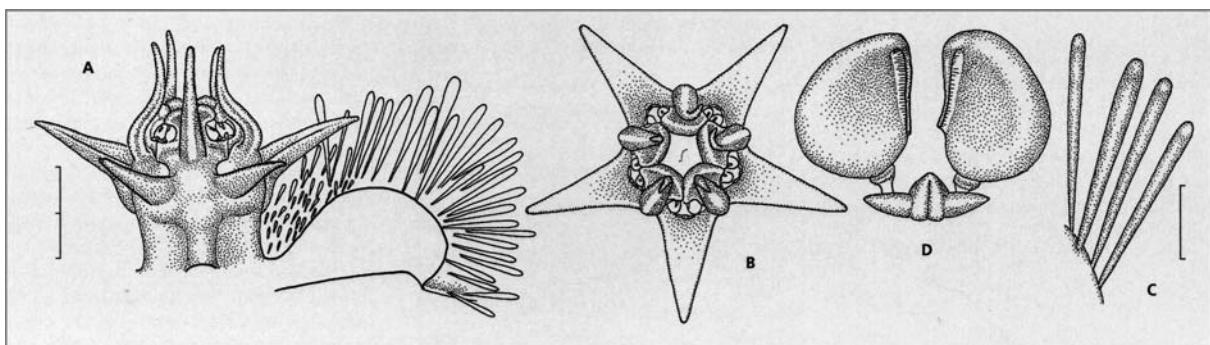


Fig. 15.42. *Stapelia glanduliflora*. A, side view of gynostegium and part of centre of corolla. B, face view of gynostegium. C, papillae inside corolla. D, pollinarium. Scale bars: A, B, 2 mm (at A); C, 1 mm; D, 0.25 mm (at C). Drawn from PVB 77, Clanwilliam.

8. *Stapelia erectiflora*

Stapelia erectiflora N.E.Br., *Gard. Chron.* Ser. 3, 6: 650 (1889).

Gonostemon erectiflorus (N.E.Br.) P.V.Heath, *Calyx* 1:19(1992).

Lectotype: South Africa, Karoo, 6 miles beyond Cedarberg, Bain sub Barkly 80 (K).

Small succulent forming dense clump 150-300 mm diam. **Stems** 40-120 mm long, 8-12 mm thick, erect, shortly pubescent, green suffused with purple; **tubercles** 2-3 mm long, joined into 4 obtuse angles along stem, stem $\pm$ square in cross-section; **leaf-rudiments** $\pm$ 1.5 mm long. **Inflorescences** pubescent, 1-4 per stem randomly distributed along it, each with 1-5 flowers developing in gradual succession on stout short peduncle < 5 mm long with deltoid bracts 1-2 mm long; **pedicel** 20-120 mm long, $\pm$ 1.5 mm thick, purplish, erect holding flower facing upwards near or above apices of stems; **sepals** 1.5-3.0 mm long, 1.5 mm broad at base, deltoid, acute, purplish. **Corolla** 9-15 mm diam. (15-20 mm when fully spread out), $\pm$ turban-shaped; outside pale pinkish dull green, with 3 raised darker longitudinal veins running down each lobe to sepals; inside $\pm$ smooth, dull brownish green to purplish with narrow transverse pale green to yellow stripes, covered from base of tube to tips of lobes (somewhat sparser inside tube) with translucent-white adpressed clavate hairs up to 1 mm long pointing towards apices of lobes sometimes interspersed with fine hairs towards tips of lobes; **tube** $\pm$ 1.5 mm deep, shallowly bowl-shaped, pentagonal, sometimes corolla thickened around mouth; **lobes** 5-6 mm long, 3.5-5.0 mm broad at base, strongly recurved and rolled back under corolla, ovate-deltate, slightly convex above. **Corona** $\pm$ 4.5 mm tall, $\pm$ 7 mm broad, raised on yellow to reddish obtusely pentagonal stipe 1 mm tall, glabrous; **outer lobes** 2-3 mm long, spreading around mouth of tube with somewhat recurved apex, oblong to rectangular or lanceolate, truncate to emarginate or acute, slightly channelled down upper surface, yellow suffused with purple especially towards tips to wholly purple; **inner lobes** (2.5-) 3.0-3.5 mm long, adpressed to backs

of anthers and usually much exceeding them to become erect and then recurved, slender, dorsiventrally flattened becoming terete above, with slightly raised dorsal ridge towards base but without wing.

Distribution and habitat

Stapelia erectiflora is mainly found in the mountains beyond the south-eastern corner of Namaqualand. It is particularly well known in the northern Cedarberg, north-east of Clanwilliam in the area between Pakhuis Pass, Botterkloof and the eastern end of the Biedouw Valley but it also occurs south of Nieuwoudtville on the edge of the escarpment. There are further records from the area around Springbok but I have been unable to confirm these.

In the Cedarberg it is often found growing in shallow soils on flat or very gently sloping sandstone slabs inhabited by small members of the succulent Aizoaceae such as various species of *Antimima* and *Conophytum* as well as much moss, lichen and several small geophytes. However, in Botterkloof the plants occur among bushes and rocks on steep, sandstone slopes.

Diagnostic features and relationships

In *S. erectiflora* the plants are extremely floriferous, bearing flowers in small clusters all along the length of the stem. The flowers are always held facing upwards on quite long pedicels. The corolla is small with the lobes folded back right behind the flower (though not very tightly) so that it has a button-like shape or resembles a 'Turk's cap', as Brown (1890:t.1921) expressed it. The inside appears to have a silvery colour but, if it is examined more carefully, it will be seen that actually this colour is mainly caused by the hairs covering it. The surface beneath the hairs is pale green to purplish and there are

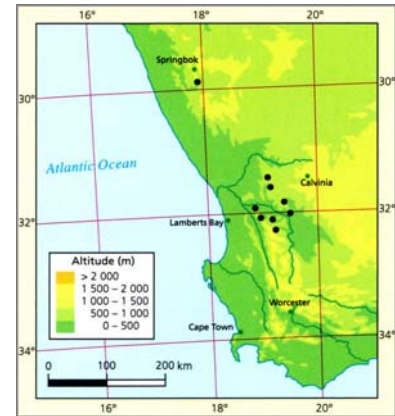


Fig. 15.43. Distribution of *Stapelia erectiflora*.

transverse bands of darker purple or brownish on this which become a little more obvious towards the tips of the lobes. The whole of the inside is covered with clavate, translucent-white hairs which are mostly pressed to the surface of the flower with their tips facing the tips of the lobes. Along the margins they tend to be a little less tightly pressed to the surface and may form more of a ragged beard. Between them there are many finer and very short, similarly coloured hairs. For the first day or so after opening the flowers emit a fruity, almost honey-like scent but after that they are odourless.

The outer corona lobes are comparatively long and usually rectangular, initially spreading and then rising upwards towards their apices. The inner corona lobes are long and slender, rising up beyond the anthers and diverging, often quite considerably.

Stapelia erectiflora and *S. glanduliflora* are closely allied species which are also probably

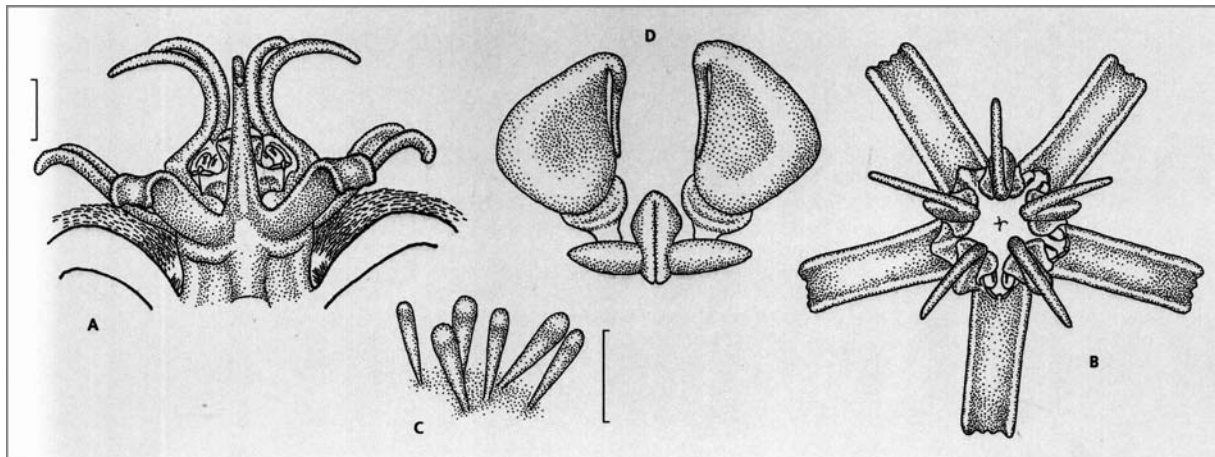


Fig. 15.44. *Stapelia erectiflora*. A, side view of centre of dissected flower. B, face view of gynostegium. C, papillae inside corolla. D, pollinarium. Scale bars: A, B, 1 mm (at A); C, 0.5 mm; D, 0.25 mm (at C). Drawn from PVB 5993, Pakhuis Pass, north-east of Clanwilliam.

STAPELIA ERECTIFLORA



Fig. 15.45. *S. erectiflora*, PVB 5993, Pakhuis Pass, northeast of Clanwilliam.

closely related to *S. paniculata*. Both are separated from all material of *S. paniculata* by the clavate hairs covering much of the inside of the corolla. These hairs are much longer in *S. glanduliflora* than in *S. erectiflora*. In *S. glanduliflora* they are quite widely spreading whereas in *S. erectiflora* they are closely adpressed to the surface of the corolla. A further difference is that *S. erectiflora* always has considerably longer corona lobes than one finds in *S. glanduliflora* where, in both the outer and inner series, the lobes are short.

Leach (1985) included some odd collections under *S. erectiflora* and this particularly applies to the material of Leach & Bayer i6172. In this gathering, and a subsequent collection made at

the same spot (PVB 6173), the flowers are held erect above the stems and the corolla lobes are somewhat reflexed, though not as tightly as is typical of *S. erectiflora*. Superficially it seems, therefore, to belong to *S. erectiflora*. The inner surface of the corolla is covered with adpressed hairs but these are not clavate and they are thickest a little above the base from where they taper gradually to their tips (fig. 28 G). The corona consists also of very short lobes. Both this and the shape of the hairs are more similar to what is known in *S. paniculata*. Geographically, material from this locality fits better into *S. paniculata* so it is excluded from *S. erectiflora* in this account.

The plants described by Leach as *S. erectiflora* var. *prostratiflora* have been shown to be hybrids between *S. erectiflora* and *S. glanduliflora* and are discussed under 'Naturally occurring hybrids'.

History

Stapelia erectiflora was described by N.E. Brown from material collected by Thomas C. Bain and sent to Kew by Henry Barkly. These plants were collected in karroid areas beyond the Cedarberg, probably on the eastern slopes of the Pakhuis Pass or towards Botterkloof.



Fig. 15.46. *S. erectiflora*, PVB 5993, Pakhuis Pass, northeast of Clanwilliam.



Fig. 15.47. *S. erectiflora*, PVB 7507, north of Clanwilliam, a large plant in habitat, May 1998.

9. *Stapelia flavopurpurea*

Stapelia flavopurpurea Marloth, Trans. S. African Philos. Soc. 18: 48, t. 5, fig. 1 (1907).

Gonostemon flavopurpurea (Marloth) P.V.Heath, *Calyx* 1:18 (1992).

Type: South Africa, Laingsburg distr., Marloth 4227 (missing).

Lectotype (selected here): Asbestos Hills, near Prieska, Marloth 5117 (PRE, holo.; GRA, iso.).

Stapelia fleckii A.Berger & Schltr., *Vierteljahrsschr. Naturf. Ges. Zürich* 53: 490 (1909).

Stapelia flavopurpurea var. *fleckii* (A.Berger & Schltr.) A.C.White & B.Sloane, *Stap.*, ed. 2, 2: 495 (1937).

Gonostemon flavopurpurea var. *fleckii* (A.Berger & Schltr.) P.V.Heath, *Calyx* 3: 8 (1993).

Lectotype (selected here): Namibia, Rehoboth, Fleck 248a (Z).

Small succulent forming diffuse clump up to 150 (-200) mm diam. **Stems** 20-60 (-100) mm long, 6-15 mm thick, decumbent, very shortly pubescent (somewhat sandpaper), deep green suffused with purple; **tubercles** 1-3 mm long, widely spaced along stem and obtusely conical, joined into 4 obtuse angles with stems square to slightly concave-sided; **leaf-rudiments** 1.0-1.5 mm long. **Inflorescences** finely pubescent, 1-several per stem near apex, each with 1-5 flowers developing in gradual succession on short erect peduncle (< 5 mm long) with few short deltoid bracts < 1 mm long; **pedicel** 15-30 mm long, 1.5 mm thick, erect, holding flower facing upwards, reddish; **sepals** 3-4 mm long, 1 mm broad at base, lanceolate, acute, reddish green. **Corolla** 25-50 mm diam., rotate; outside finely scabrous, pale reddish green to cream at base with 1-3 prominent (not raised) longitudinal veins on each lobe; inside heavily transversely rugose on lobes fading towards ± smooth centre (sometimes rugose only near tips), green, yellow, brown or pale red on lobes changing abruptly just below bases to white where covered



Fig. 15.48. *S. flavopurpurea*, PVB 5138, west of Strydenburg.

ered (though not densely) with translucent white to dark purple clavate hairs (< 0.5 mm long, becoming shorter in tube and vanishing ± halfway down); **tube** 1.5-2.0 mm long, 5-8 mm broad, enclosing corona closely towards base, cupular, pentagonal, with corolla slightly thickened around mouth; **lobes** 10-23 mm long, 4-6 mm broad at base, spreading, narrowly ovate to lanceolate, acute, strongly convex above from reflexed ciliate margins. **Corona** ± 9-10 mm tall, ± 10 mm broad, raised on slight stipe, glabrous and shiny; **outer lobes** 2-3 mm long, 1.0-1.5 mm broad, steeply ascending, rectangular, truncate and prominently apiculate, red-purple to white and pink-edged, becoming yellowish towards base, with sides incurved so deeply channelled; **inner lobes** 6-9 mm long, adpressed to backs of anthers then connivent-erect then recurved, dorsiventrally flattened and broad at base so ± completely hiding anthers and pollinia, then becoming slender terete with slightly swollen apex, with ascending narrowly deltoid and laterally flattened dorsal wing 4-5 mm long, red-purple to white suffused with pink.

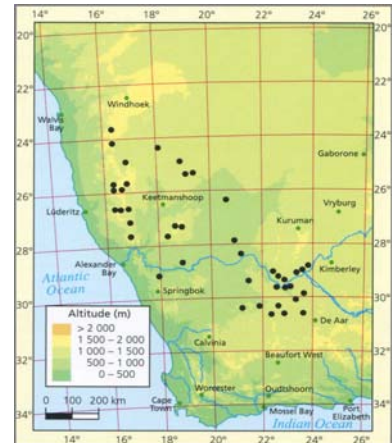


Fig. 15.49. Distribution of *Stapelia flavopurpurea*.

Distribution and habitat

Stapelia flavopurpurea has a wide distribution in Namibia and South Africa. In Namibia plants have been found from Nauchas, a little south-west of Windhoek, across a broad swathe of arid territory southwards to near Witpiitz and eastwards to Warmbad, i.e. generally west of the Kalahari sands and east of the Namib proper and also outside the winter-rainfall zone in the south-west. In South Africa it is found from Twee Rivieren southwards via Upington, Kenhardt and Carnarvon to near Britstown. There are two records from the eastern side of the Kamiesberg, but generally it keeps well east of the winter-rainfall region.

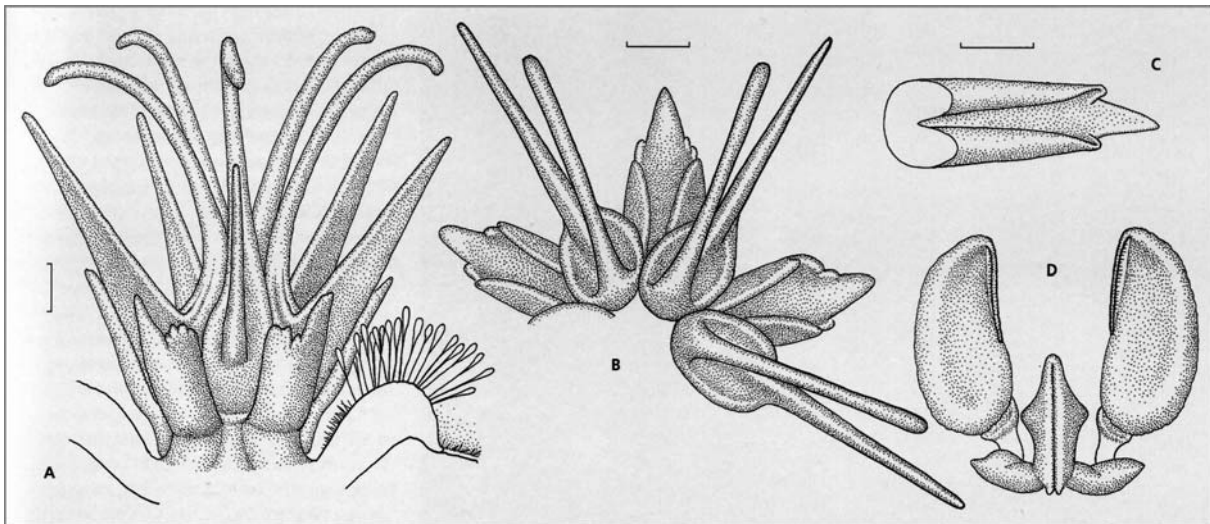


Fig. 15.50. *Stapelia flavopurpurea*. A, side view of gynostegium and part of centre of corolla. B, face view of part of gynostegium. C, face view of outer corona lobe. D, pollinarium. Scale bars: A, 1 mm; B, 1 mm; C, 1 mm; D, 0.25 mm (at C). Drawn from: A, D, *De Villiers*, Vaalputz, Gamoep; B, PVB 8152, Vrede, Warmbad, Namibia; C, PVB 7198, north-east of Witpiitz, Namibia.

STAPELIA FLAVOPURPUREA

Although found in a variety of soils over this wide area, *S. flavopurpurea* is particularly often encountered on calcretes where it grows among stones and under small, stunted bushes. In the area from Upington to Britstown it is quite often found in such habitats together with *Tridentea jucunda*. Plants quite frequently grow around the bases of shrubs of the *driedoring*, *Rhigozum trichotomum*.

Diagnostic features and relationships

The stems of *S. flavopurpurea* are mostly quite short, relatively stout and are square in cross-section with a tendency to taper evenly towards the apex. They have a distinctive, uniformly deep green colour suffused with purple and

a somewhat sandpapery texture, rather than the usual pubescence. The leaf-rudiments are quite obvious but they are small and very slightly spreading.

Flowers are produced near the tips of the stems, often in several small clusters per stem and they are held facing upwards. As a consequence, they often project above the plant and, when a floriferous specimen is growing well concealed in a shrub, the flowers may be all that can be seen of it. Mostly they are bright yellow inside but they have been recorded in shades of yellow, green, red or brown. The lobes have their margins strongly folded back so that they are narrow and convex above. They are usually densely and coarsely transversely rugose and without hairs, although a few plants have been encountered around Witpütz in Namibia where they are rugose only towards the tips of the lobes and the rest of the inner surface is more or less smooth. At the base of the lobes the inside of the corolla suddenly becomes smooth and changes to white. Here it is covered quite densely with a beard of more or less erect, clavate, translucent, white to purple hairs which become shorter in the tube and fade away around its middle. When these are purplish, they lend a purplish hue to the centre of the corolla and this is often matched by a suffusion of pink in the corona. As is often the case in the more or less flat-flowered species of *Stapelia*, the tube consists of a short depression in the centre which surrounds the base of the gynostegium quite closely.

In the centre of the flower there is a tall and complicated-looking gynostegium. The relatively short outer corona lobes ascend fairly steeply, with the sides folded inwards to form a more-than-usually deep and narrow channel. The inner corona lobes are noticeably broad just above the base and this part covers the anthers and the pollinia almost entirely. Access to the pollinia and guide-rails is therefore extremely restricted. However, the pollinia are fairly long and narrow, which suits this arrangement (as happens also in *Tromotriche baylissii* and *T. choanantha*). In most cases the corona lobes are shiny, translucent whitish and faintly edged with pink (becoming yellow towards the base in the outer lobes) or pale pinkish purple. In material from around Witpütz they are all a good deal darker, with an edging of purple-red. In all cases the colour of the various corona lobes contrasts usually quite markedly with the colour of the corolla lobes and this contrast of colours may have been the reason for Marloth's name.

Such exotic colours as are found here on the corolla and corona are otherwise entirely unknown in *Stapelia*. The only other stapeliad with comparable colours on the corolla is *Tridentea virescens*, where the flowers have a foul, excrement-like smell and the corona is differently shaped. In *S. flavopurpurea* the odour of the flowers varies from pleasantly and strongly



Fig. 15.51. *S. flavopurpurea*, PVB 7198, north-east of Witpütz, Namibia, flowers rather less rugose than usual.



Fig. 15.52. *S. flavopurpurea*, PVB 5635, Nauchas, Namibia, in habitat, March 1993.a



Fig. 15.53. *S. flavopurpurea*, PVB 5424, north-west of Vosburg.



Fig. 15.54. *S. flavopurpurea*, PVB 5635, Nauchas, Namibia, a plant with unusually dark flowers, in habitat, March 1993.

honey-like (as first noted by Dinter, 1914, p. 52) or scented like marzipan in yellow ones, to faintly evil in darker reddish or brownish flowers. It is remarkable that within a single species there should be such a wide range of odours and, of course, a *Stapelia* whose flowers are occasionally sweet smelling is also a welcome change.

History

Stapelia flavopurpurea was first collected in January 1890 near Rehoboth by Eduard Fleck, who was a geologist and an official of the German Colonial Company. As with most of Fleck's collections, these are preserved at Zurich (Z). The material on which the name *S. flavopurpurea* was based was reputed to have been collected in the Laingsburg district by Rudolf Marloth and it flowered in his garden for the first time in March 1906 (Marloth 1907). However, this is now accepted as being an unlikely locality for this species as it has been collected in recent years only much further to the north and east. Marloth made several collections of *S. flavopurpurea* in the Asbestos Mountains north of Prieska and it is probable that his original collection was made around there too.

Fleck's Namibian material was described, somewhat later than *S. flavopurpurea*, by Alwyn Berger and Rudolf Schlechter as a separate species, *S. fleckii*. Dinter (1914) suggested that *S. fleckii* was possibly synonymous with *S. flavopurpurea*, while White & Sloane (1937) regarded it as a variety of *S. flavopurpurea* and Leach (1985) abandoned the name entirely.

10. *Stapelia acuminata*

Stapelia acuminata Masson, *Stap. Nov.*: 15, t.17 (1797).

Gonostemon acuminatus (Masson) P.V.Heath, *Calyx* 1:18 (1992).

Type: South Africa, Cape, Little Namaqualand, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 17.

Stapelia acuminata var. *brevicuspis* N.E.Br., *Fl. Cap.* 4 (1): 965 (1909).

Gonostemon acuminatus var. *brevicuspis* (N.E.Br.) P.V.Heath, *Calyx* 3:8 (1993).

Type: Cape, Okiep, Templeman sub N.S Pillans 26 (BOL).

Stapelia inducta Nel, *Sukkulantenkunde* 2:33 (1948).

Type: Cape, Namaqualand, Nuwerus, Nel 415 (missing).

Small succulent forming diffuse clump 150-500 mm diam. with few relatively stout stems. **Stems** 50-200 mm long, 8-15 mm thick, decumbent, shortly pubescent, green suffused with purple; **tubercles** 3-5 mm long, widely spaced along stem and obtusely conical, usually joined into 4 obtuse angles and stems $\pm$ square in cross-section; **leaf-rudiments** 1.5 mm long. **Inflorescences** pubescent, 1-3 per stem, randomly distributed along sides of stems, each with 1-5 flowers developing in rapid succession on short stout peduncle < 5 mm long; **pedicels** 3-6 mm long, 1.5-2.0 mm thick, purplish, spreading and holding flower facing horizontally or upwards; **sepals** 2.5-5.0 mm long, 2 mm broad at base, ovate, acute, purplish to green. **Corolla** 17-40 mm diam., rotate; outside yellow-green to purplish, usually with 1-3 prominent (not raised) longitudinal veins on each lobe; inside finely transversely rugulose, upper surface of these ruguloses yellow to white except towards tips of lobes, rest red- to dark purple-brown, glabrous to finely pubescent towards margins; **tube** $\pm$ 1.5 mm long, 4 mm broad, pentagonal, broadly V-shaped and coming close to stipe near base only; **lobes** 8-12 mm long, 6-8 mm broad at base, ascending to spreading, ovate, acuminate to acute, convex above from revolute margins usually adorned with straight white cilia up to 2 mm long. **Corona** $\pm$ 6.5 mm tall, $\pm$ 8 mm broad, raised on obtusely pentagonal stipe 1-2 mm long; **outer lobes** 2-3 mm long, $\pm$ 1.5 mm broad, spreading to ascending, oblong to $\pm$ rectangular usually narrowing slightly towards truncate-emarginate to bilobed apex, orange-brown to purplish (sometimes red-spotted on yellow), slightly channelled down middle; **inner lobes** 3-5 mm long, adpressed to backs of anthers then connivent-erect in column above style-apex and recurved above, dorsiventrally flattened towards base becoming terete above, with spreading laterally flattened $\pm$ deltoid dorsal wing near base, cream- to yellow-spotted and striped with brown to red towards base.

Distribution and habitat

Stapelia acuminata is only found in Namaqualand, where it is fairly frequent in the Kamiesberg, particularly around Kamieskroon. A single record, made in 1899 by Robert Templeman, is known from further north at Okiep. Further to the south it is of sporadic occurrence on the

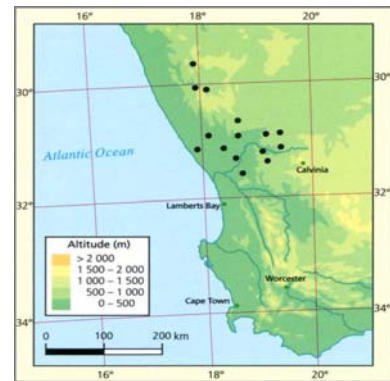


Fig. 15.55. Distribution of *Stapelia acuminata*.

Knervslakte from Bitterfontein to near Vanrhynsdorp and it is somewhat more frequent on the slopes along the eastern boundaries of the Knervslakte from Kliprand south-eastwards via the Langberg and Kubiskow to Loeriesfontein and north of Nieuwoudtville. As far as is known, *S. acuminata* does not grow either in the coastal parts of Namaqualand or in the very dry north-west (i.e. in the Richtersveld).

Plants are found under bushes on gravelly ground or between rocks. Occasionally they occur under small bushes in shallow pockets of soil on granite domes. In the Kamiesberg they are often associated with disturbed areas overgrown with *Galenia africana*. On the Knervslakte they occur not on the well-known patches of quartz gravel but rather in the more bushy areas between them or on hillsides.



Fig. 15.56. *S. acuminata*, PVB 6071, south-west of Loeriesfontein.

STAPELIA ACUMINATA

Diagnostic features and relationships

Stapelia acuminata forms clumps of stems up to 0.5 m in diameter, which are usually somewhat diffusely decumbent and are not tightly clustered. The stems are velvety, usually suffused with purple and mostly regularly 4-angled but with a distinct groove along the stem between the angles.

Flowers are produced on peduncles that are randomly distributed along the stems but are often towards the base. The pedicels are relatively short and several flowers may mature soon after each other on each peduncle, so that small clusters of open flowers develop. At around 30 mm in diameter, the flowers are of medium size. Usually they are more or less flat, with a small depression in the centre forming a short, pentagonal tube around the base of the gynostegium and with the lobes tapering to slender tips. The inside is covered quite densely with fine, smooth, transverse ridges and the upper surface of these ridges is yellowish, while the ground colour between them is red- to purple-brown. Beyond their middle, the lobes become plain purple-brown, but the yellow markings increase in intensity towards the centre of the flower with the result that the whole of the flower has a rather paler colour towards the middle. Hairs are absent from the inside of the flower and are only found as a usually conspicuous white fringe along the margins of the lobes.

In *S. acuminata* the corona is comparatively large. As it is brownish or purplish, it is quite a bit darker than the surrounding parts of the corolla and contrasts strongly with it. It is raised on a pentagonal stipe, with the almost rectangular outer lobes often spreading to the surface of the corolla just outside the tube and slightly channelled on their upper surface. The inner lobes are comparatively long, connivent in the centre then diverging, and each has the usual flattened dorsal wing near the base.

In terms of the size of the flower, *S. acuminata* bears some resemblance to *S. cedrimontana*, differing from it by the finer, transverse mottling of yellow and the considerably shorter



Fig. 15.57. *S. acuminata*, Nagel 202, Sout River, north of Vanrhynsdorp.



Fig. 15.58. *S. acuminata*, PVB 6078, north-west of Loeriesfontein.

pedicels which hold the flower close to the stem. Leach (1985) also compared it with *S. arenosa*. In *S. arenosa* the corolla is generally much more deeply rugulose and darker on the lobes, it is mostly markedly more thickened around the corona and the shape of the corona lobes is different. The two species have been observed growing together north of Nieuwoudtville and here a few specimens somewhat intermediate between them were observed. Whether these were hybrids or evidence of intergradation has not been established.

History

Stapelia acuminata was discovered by Francis Masson somewhere in Namaqualand and flowered in his little garden at Cape Town in 1791.

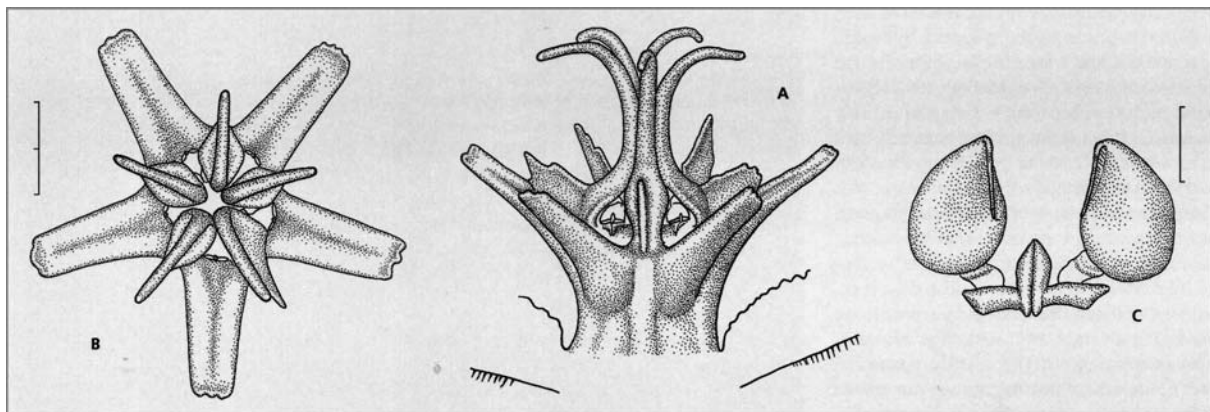


Fig. 15.59. *Stapelia acuminata*. A, side view of gynostegium and part of centre of corolla. B, face view of gynostegium. C, pollinarium. Scale bars: A, B, 2 mm (at B); C, 0.25 mm. Drawn from PVB, Loeriesfontein.

11. *Stapelia paniculata*

Stapelia paniculata Willd., Enum. PL, Suppl.: 13-14 (1813-14).
Tridentea paniculata (Willd.) Schult. ex G.Don., Gen. Hist. 4:118(1837-38).
Stapelia concinna var. *paniculata* (Willd.) N.E.Br., Fl. Cap. 4 (1): 969 (1909).
Gonostemon paniculatus (Willd.) P.V.Heath, Calyx 1: 19 (1992).
Type: South Africa, Masson? (B-W).

Dwarf succulent forming neat compact clump 60-150 mm diam. **Stems** 20-150 mm long, 3-12 mm thick, erect, shortly pubescent, green often mottled with purple; **tubercles** 2-4 mm long, low conical, joined into 4 obtuse angles along stem between which stem slightly grooved; **leaf-rudiments** 1.0-1.5 mm long. **Inflorescences** finely pubescent, 1-5 per stem from base to apex, each with 1-10 flowers developing in close succession on short peduncle up to 5 mm long with several deltoid bracts 1.0-1.5 mm long; **pedicel** 9-22 mm long, 1.5 mm thick, spreading with ascending tip to ascending, usually holding flower facing at least somewhat upwards; **sepals** 3-4 mm long, 1.5 mm broad at base, lanceolate, acute, green to reddish. **Corolla** 15-25 mm diam., rotate; outside reddish green with 1-5 darker veins on each lobe; inside usually obscurely transversely rugulose at least from middle of lobes downwards to base of tube (sometimes all over), red-purple to dark maroon sometimes transversely lined with yellow around and below bases of lobes, covered with sharp-tipped spreading to adpressed purple to white hairs over most of surface (often disappearing towards tips of lobes, sometimes very short all over) longest towards margins of lobes and often translucent-white there; **tube** ± 1 mm deep, very short and broadly bowl-shaped, pentagonal, with corolla somewhat thickened around mouth; **lobes** 5-9 mm long, 4-5 mm broad at base, spreading to reflexed, ovate-acuminate. **Corona** 2.5-5.0 mm tall, 4.5-7.0 mm broad, raised on obtusely pentagonal reddish stipe ± 1 mm long, glabrous; **outer lobes** 1.0-1.5 mm long and slightly narrower, ascending-spreading, ± rectangular with 1-3 obtuse teeth at apex, dark maroon; **inner lobes** 1.0-2.6 mm long, dark maroon, adpressed to backs of anthers then erect to recurved beyond them, dorsiventrally flattened below becoming terete above, narrowly acuminate, usually with ± deltoid obtuse laterally flattened and ascending dorsal wing.

The complexities involved in trying to separate the 'species' *S. immelmaniae*, *S. kougabergensis*, *S. paniculata* and *S. scitula* (Leach 1985) suggest that not all are actually distinct.
As far as *S. paniculata* and *S. scitula* are concerned, in *S. paniculata* (especially around

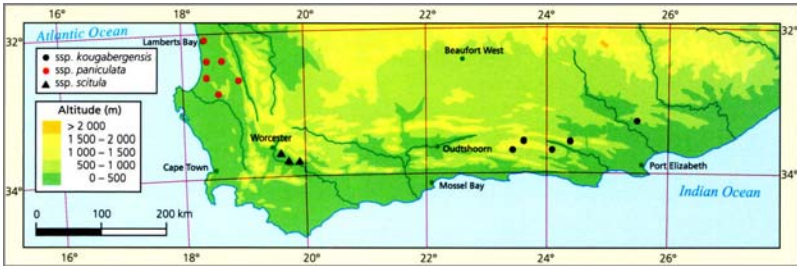


Fig. 15.60. Distribution of *Stapelia paniculata*.

Lambert's Bay) plants may also have small stems packed into a 'neat' plant as is typical of *S. scitula*, but in material from south of Lambert's Bay they are much more laxly clump-forming with longer and much stouter stems. However, from *S. paniculata*, *S. scitula* is 'immediately distinguished when in flower by its much shorter outer corona lobes and entirely different corolla indumentum' (Leach 1985: 118). In *S. paniculata* the outer corona lobes are 2.0-2.5 mm long (1.0-1.5 mm in *S. scitula*) and in so variable an organ as this is in *Stapelia*, this is a negligible difference. In *S. scitula* the hairs on the inside of the corolla are erect to spreading, sharp-pointed and usually purple, though in some flowers they are very pale. They vary from less than 1 mm to nearly 2 mm long and are longest towards the margins of the lobes.

In *S. paniculata* the hairs are exactly as above but are translucent-white. In specimens from Lambert's Bay they may be slightly thicker towards the base. However, in material from Klein Tafelberg cited by Leach (1985) under *S. paniculata*, they differ from those of *S. scitula* purely in colour. In particular, in material from this locality there is no 'dense margin of stout white hairs which is characteristic of the species' (Leach 1985:124). There appear, therefore, to be no clear-cut differences between *S. scitula* and *S. paniculata* and, in particular, there is no evidence of an 'entirely different' corolla-indumentum in the two.

In the cases of *S. scitula* and *S. immelmaniae*, *S. scitula* was supposed to differ from *S. immelmaniae* by the small stems ('small neat habit'), inflorescence usually developed from near the base of the stems (randomly produced in *S. immelmaniae*), smaller flowers on relatively longer pedicels and usually held erect, and outer corona lobes 'less than half the

length of those of *S. immelmaniae*' (Leach 1985: 118). Investigation of more material has shown that in *S. scitula* the inflorescence may arise anywhere on the stem and, especially in stems with several inflorescences, one or more of them lies near the apex, the outer corona lobes are 1.0-1.5 mm long and those in *S. immelmaniae* are 2 mm long, so there is not such a strong difference here as suggested by Leach. In addition, in his fig. 94 of *S. immelmaniae*, the flower is held erect on a pedicel almost as long as the flower is broad. This is very similar to *S. scitula* where the pedicel varies from 9-22 mm long and most of the flowers are 15-18 mm in diameter. *Stapelia scitula* and *S. immelmaniae* are therefore distinguished by the smaller stems and flowers in *S. scitula*.

Leach (1985: 122) compared *S. kougabergensis* with *S. acuminata*. However, the main problem is to separate it from *S. scitula*. In some collections of *S. kougabergensis* (e.g. PVB 1161) the stems are just as small and slender as they always are in *S. scitula* and may also be in *S. paniculata*. In many collections of *S. kougabergensis* the inside of the flower is almost entirely glabrous but some exist (e.g. PVB 1161) where they are pilose, mainly towards the margins of the lobes. In *S. scitula* the inside of the flower is always quite densely hairy and this is the only difference between them.

Stapelia paniculata occurs in several places very near to *S. cedrimontana* and, although this is not shown by the cladogram presented here, they may well be closely related. The plants described as *S. montana* are especially hard to place in either species. The stems of *S. paniculata* are always finely pubescent whereas those of *S. cedrimontana* are more or less glabrous and, for this reason (and despite some closely matching flowers in some plants of '*S. montana*' and *S. paniculata*), '*S. montana*' is placed under *S. cedrimontana*.

Here a broad view is taken of this complex and both *S. kougabergensis* and *S. scitula* are treated as subspecies of *S. paniculata*.

Key to the subspecies of *S. paniculata*

- 1. Corolla lobes longer than broad 2.
- 2. Inside of corolla with fine ± erect hairs 11b. subsp. *scitula*
- 2. Inside of corolla with slightly thickened hairs ± adpressed to surface of corolla 11a. subsp. *paniculata*
- 1. Corolla lobes ± as long as broad 11c. subsp. *kougabergensis*

STAPELIA PANICULATA

11a. *Stapelia paniculata* subsp. *paniculata*

Stapelia immelmaniae Pillans, *S. African Gard. & Country Life* 18: 62 (1928, special reprint).

Type: Cape, Piketberg, *Immelman sub* NBG 581/26 (BOL).

Stapelia nouhuysii E. Phillips, *Fl. Pl. South Africa* 9: t. 345 (1929).

Type: Cape, Lambert's Bay, *J. J. van Nouhuys sub* PRE 8027 (PRE).

Corolla inside with hairs adpressed to or nearly adpressed to surface, usually somewhat thickened towards bases; **lobes** longer than broad.

Distribution and habitat

Subsp. *paniculata* is known from several somewhat dispersed localities from Lambert's Bay (where much of the former habitat was destroyed by quarrying of rock for the Saldanha-Sishen railway line) southwards to the northern edges of the Piketberg and also from a collection in Piekenierskloof

Pass near Citrusdal. Leach (1985) also cited a specimen from between Loeriesfontein and Nieuwoudtville but this subspecies is unlikely to occur there and this record is omitted from the distribution map (fig. 15.60).

Plants of this subspecies are always found on soils derived from sandstones, usually on flat ledges on outcrops of rock, where they grow with other succulents in shallow soils between stones and small bushes surrounded by fynbos.

Diagnostic features and relationships

Around Lambert's Bay, specimens of subsp. *paniculata* have small, slender stems mostly 5-7 mm thick, which are tightly packed into clumps. Further south, around Verlorenvlei and on the Klein Tafelberg, the stems are much thicker (6-10 mm) and reach 150 mm tall and also form more loosely packed clusters.

Near Lambert's Bay the flowers are usually borne near the base of the stem and face outwards. In material from further south, the



Fig. 15.61. *S. paniculata* subsp. *paniculata*, PVB 4739, near Elands Bay.

stems produce up to five inflorescences each and these arise from near the base to close to the apex. In such plants the flowers face upwards.

In subsp. *paniculata* the inside of the flower is red to purplish, often with obscure, transverse paler lines. This is very variably obscured by a covering of hairs which are mostly longer and denser towards the margins of the lobes. In some the hairs are particularly dense and then the flower is more or less silvery, while more commonly the hairs let through some of the background colour so that the flower is pale pink. At two localities (PVB 4739, 6173) some plants were found where the hairs were mainly confined to the central, united part of the corolla and in these the underlying markings of the surface were clearly visible. In some of those with the flowers facing upwards, the hairs were not closely adpressed to the surface of the corolla and these are hard to distinguish from material from the Piketberg formerly known as *S. immelmaniae*. In others the hairs are closely adpressed to the surface and occasionally the lobes are short and reflexed behind the corolla as well so that altogether these have a marked similarity to flowers of *S. erectiflora*.

History

Plants named originally *S. paniculata* have a somewhat obscure history and it is not known who introduced them to England or exactly when this happened, though they were in cultivation before 1813. This suggests that Francis Masson might have collected them.



Fig. 15.62. *S. paniculata* subsp. *paniculata*, PVB 6173, Paleisheuvel. At this locality the flowers resemble those of *S. erectiflora*, with the corolla lobes folded back behind the flower.

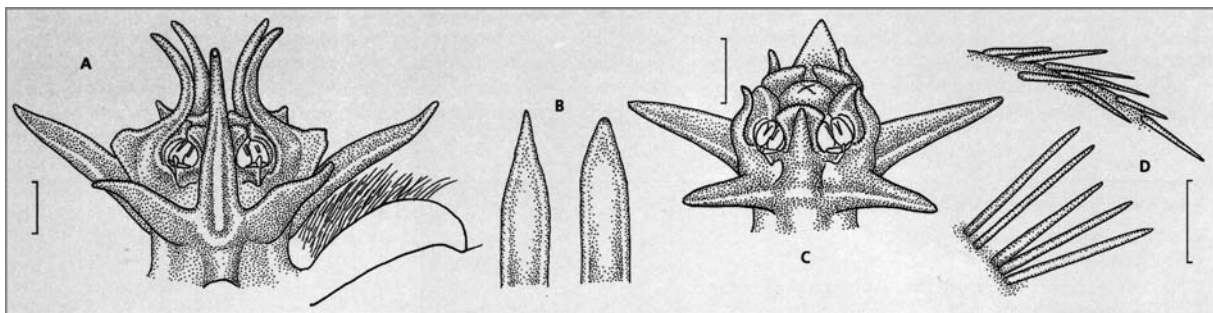


Fig. 15.63. *Stapelia paniculata* subsp. *paniculata*. A, side view of gynostegium. B, face view of outer corona lobes. C, oblique view of gynostegium. D, papillae inside corolla. Scale bars: A, B, 1 mm (at A); C, 1 mm; D, 0.5 mm. Drawn from A, B, PVB 4739, near Elands Bay; C, D (upper), PVB 6173, Paleisheuvel; D (lower), PVB 6380, Klein Tafelberg.



Fig. 15.64. *S. paniculata* subsp. *paniculata*, PVB 4739, near Elands Bay. Flowers such as this are not distinguishable from '*S. immelmaniae*'.



Fig. 15.65. *S. paniculata* subsp. *paniculata*, PVB 4739, near Elands Bay, a plant with especially densely hairy flowers.



Fig. 15.66. *S. paniculata* subsp. *paniculata*, PVB 4739, near Elands Bay.



Fig. 15.67. *S. paniculata* subsp. *paniculata*, PVB 6380, Klein Tafelberg, south of Lambert's Bay



Fig. 15.68. *S. paniculata* subsp. *paniculata*, PVB 1446, east of Lambert's Bay. This is the old plant which was known to Carl Lückhoff, in habitat, May 1977.

STAPELIA PANICULATA

11b. *Stapelia paniculata* subsp. *scitula*

Stapelia paniculata subsp. *scitula* (L.C.Leach)

Bruyns, comb. et stat. nov.

Stapelia scitula L.C.Leach, S. African J. Bot. 3:174 (1984).

Gonostemon scitulus (L.C.Leach) P.V.Heath, *Calyx* 1: 19 (1992).

Type: South Africa, Cape, Buitenstekloof, Langvlei, Leach & Bayer 15845 (PRE, holo.; B, K, NBG, SRGH, iso.).

Corolla inside with $\pm$ erect to slightly forward-tilted fine hairs; lobes longer than broad.

Distribution and habitat

Subsp. *scitula* occurs for a distance of about 30 km parallel to the Langeberg in the eastern part of the Worcester-Robertson Karoo. It has been observed on the hills both to the south and to the north of Langvlei, on steep north-facing slopes north-east of Robertson and on hills near Goudmyn, to the south-east of Robertson. Plants are usually of quite scattered occurrence among stones and under small bushes (particularly under shrubs of *Pteronia paniculata* and *P. fastigiata*), usually on steep and stony, shale or dolomitic slopes.

Diagnostic features and relationships

Specimens of subsp. *scitula* usually have extremely slender stems (3–4 mm in diameter) packed into dense neat clumps. In cultivation some of these slender stems may swell out to anything between 5 and 8 mm thick, although most of them remain noticeably more slender than is typical of *Stapelia*.

In subsp. *scitula* the flowers always have a maroon colour which varies somewhat in intensity and also varies quite considerably in the presence or absence and intensity of transverse yellow lines. Hairs are usually quite coarse and purple on the inside of the flower but do not obscure the colour of the corolla. Some plants have been seen where they are very fine, purple and scattered on the face of the corolla whereas in others they are translucent-



Fig. 15.71. *S. paniculata* subsp. *scitula*, PVB 6370, north-east of Robertson.



Fig. 15.69. *S. paniculata* subsp. *scitula*, PVB 1403, west of Robertson.

white, as well as denser and longer towards the margins. The corolla is mostly dull-coloured but in a few the centre, although still covered with hairs, is somewhat shiny and smooth.

History

Subsp. *scitula* was first collected before 1960 in the hills near Langvlei, west of Robertson by Lily Littlewood (5 September 1921–17 July



Fig. 15.70. *S. paniculata* subsp. *scitula*, PVB 6790, south-east of Robertson.

1992). Mrs. Littlewood (nee Mayes) was born in Yorkshire and later learnt bookbinding, which she practised for a time in Worcester after her husband's untimely death in 1967 (M.C. Littlewood, pers. comm. 2001).

For some time this locality was assumed to be the only place where subsp. *scitula* grew but recent exploration has revealed its presence much more widely in the hills around Robertson.



Fig. 15.72. *S. paniculata* subsp. *scitula*, PVB 1403, west of Robertson.

11c. *Stapelia paniculata* subsp. *kougabergensis*

Stapelia paniculata subsp. *kougabergensis*

(L.C.Leach) Bruyns, *comb. et stat. nov.*

Stapelia kougabergensis L.C.Leach, *S. African J. Bot.* 3:176(1984).

Gonostemon kougabergensis (L.C.Leach) P.V.Heath, *Calyx* 1:19 (1992).

Type: South Africa, Cape, Bo-Kouga, Leach & Bayliss 15659 (PRE, holo.; K, NBG, iso.).

Corolla inside with few $\pm$ erect hairs to $\pm$ glabrous; **lobes** $\pm$ as broad as long.

Distribution and habitat

Subsp. *kougabergensis* is known in a few places in the western part of the Long Kloof around Saptou, in the western part of the Baviaanskloof, in the mountains south of Steytlerville and also at the western end of the Suurberg. Although it has not been found growing socially with any of *S. grandiflora*, *S. hirsuta* and *S. obducta*, these species often occur nearby.

Plants of subsp. *kougabergensis* are always found on soils derived from sandstones. They grow in shallow soils on outcrops of rock, mostly in the open and only rarely sheltered by small bushes. Some records from the Baviaanskloof are from an altitude of nearly 950 m, which is unusually high for a stapeliad in this region.

Diagnostic features and relationships

At the western end of the Baviaanskloof, the stems of subsp. *kougabergensis* are short and slender and rather like those of subsp. *scitula*. However, in most other places they are rather thicker (8–12 mm) and may be up to 80 mm or more tall. They are always quite obviously pubescent, unlike those in *S. obducta* or some forms of *S. hirsuta* which occur in the same general area, where they are nearly glabrous.

The flowers are mostly quite small and are usually borne near the bases of the stems. Inside, the background colour may be anything

from dark purple to brick-red and dull to shiny. Towards the bases of the lobes and below them there are usually a few irregular, transverse pale yellow bars, but these may even be dense, in which case the flower looks like a small version of that of *S. villetiae*. Some of the more boldly coloured ones emit a slight unpleasant odour (e.g. PVB 6326). Generally the inside of the flower is more or less devoid of hairs but in some specimens it is quite clearly hairy and these are very similar to flowers found in subsp. *scitula*.

The corona lobes are extremely variable, as is usual in *Stapelia*, and while the inner lobes normally rise beyond the end of the anthers,



Fig. 15.73. *S. paniculata* subsp. *kougabergensis*, PVB 6326, Groot Winterhoek Mountains, south of Steytlerville.

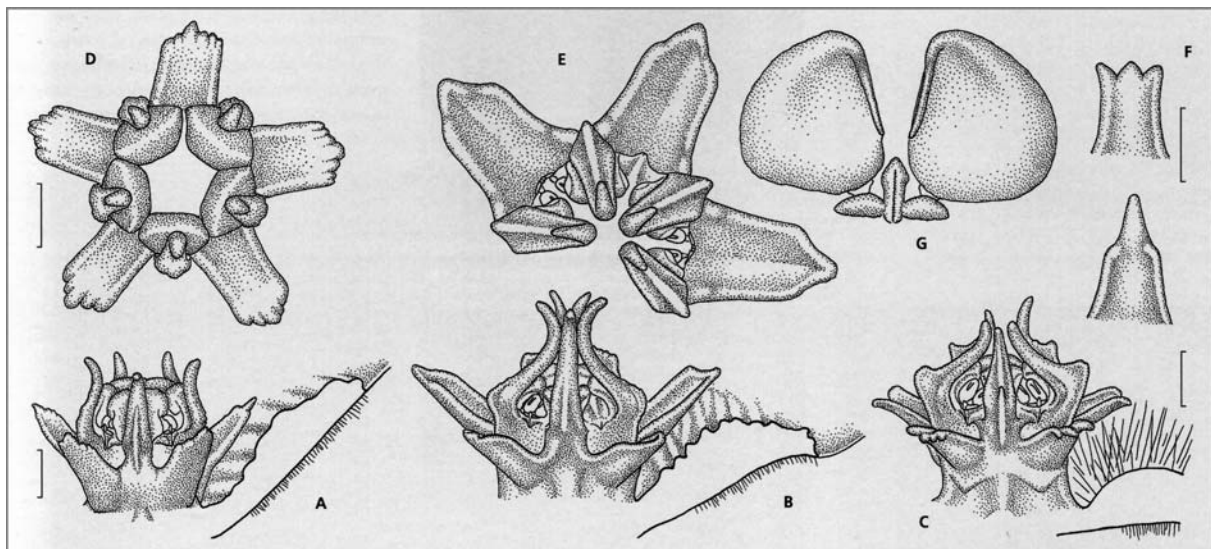


Fig. 15.74. *Stapelia paniculata* (A, B, D, E, G, subsp. *kougabergensis*; C, F, subsp. *scitula*). A–C, side view of gynostegium with part of centre of corolla. D, E, face view of gynostegium. F, face view of outer corona lobes. G, pollinarium. Scale bars: A, B, 1 mm (at A); C, 1 mm; D, E, 1 mm (at D); F, 1 mm; G, 0.25 mm (at F). Drawn from A, D, G, PVB 1891, Kouga Mountains, south of Studtis; B, E, PVB 6326, Groot Winterhoek Mountains, south of Steytlerville; C, F, PVB 6370, north-east of Robertson.

STAPELIA ARENOSA

they sometimes meet in the centre and form a column. In material from the Baviaanskloof the inner corona lobes are dorsally keeled but have almost no dorsal horn. Those from the western end of the Suurburg, on the other hand, have quite significant, laterally flattened dorsal horns, often nearly as long as the lobes themselves. These plants also have less obviously pubescent stems than is usual for *S. paniculata*, but the very small flowers suggest that this is where they belong.

History

Subsp. *kougabergensis* seems to have been collected for the first time in 1973 by Roy D.A. Bayliss and these plants were found along a hiking trail in the mountains of the upper valley of the Kouga River near Saptou, east of Uniondale and near the Long Kloof.



Fig. 15.75. *S. paniculata* subsp. *kougabergensis*, PVB 5005, Suurburg, west of Grahamstown.



Fig. 15.76. *S. paniculata* subsp. *kougabergensis*, PVB 1891, Kouga Mountains, south of Studtis.



Fig. 15.78. *S. paniculata* subsp. *kougabergensis*, PVB 1891, Kouga Mountains, south of Studtis.



Fig. 15.77. *S. paniculata* subsp. *kougabergensis*, PVB 1611, Nuwekloof, south-east of Willowmore.



Fig. 15.79. *S. paniculata* subsp. *kougabergensis*, PVB 5005, Suurburg, west of Grahamstown, the flower in this plant is remarkably similar to that in subsp. *scitula*.

12. *Stapelia arenosa*

Stapelia arenosa C.A.Luckh., *S. African Gard. & Country Life* 25: 96 (1935).

Gonostemon arenosus (C.A.Luckh.) P.V.Heath, *Calyx* 1:19(1992).

Type: South Africa, Cape, Botterkloof, *Beukman sub Lückhoff* 224 (BOL).

Stapelia beukmanii C.A.Luckh., *S. African Gard. & Country Life* 25: 96 (1935), *nom. illegit*, *non* C.A.Luckh. (1934).

Stapelia stultitoides C.A.Lückh. in A.C. White & B. Sloane, *Stap.*, ed. 2, 2: 452 (1937).

Type: Cape, Botterkloof, *Beukman sub Lückhoff* 225 (BOL).

Small succulent forming diffuse clump 150-300 mm diam. with few relatively stout stems. **Stems** 50-200 mm long, 8-15 mm thick, decumbent, shortly pubescent, green suffused with purple; **tubercles** 3-5 mm long, widely spaced along stem and obtusely conical, sometimes joined into 4 obtuse angles (sometimes with groove between them) and then stem $\pm$ square in cross-section, randomly arranged along flowering stem; **leaf-rudiments** $\pm$ 1.5 mm long. **Inflorescences** pubescent, 1-6 per stem mainly in upper half (but occasionally lower), each with 2-8 flowers opening in close succession (often with 2 or more open together) on short stout peduncle $<$ 5 mm long; **pedicel** 2-6 mm long, 1.5-2.0 mm thick, purplish, spreading and holding flower facing horizontally or upwards; **sepals** 3-5 mm long, 1.5-2.0 mm broad at base, lanceolate, purplish. **Corolla** 25-35 mm diam., rotate; outside green to purplish usually with 1-3 prominent (not raised) longitudinal veins on each lobe; inside densely and irregularly but $\pm$ transversely rugulose, upper surfaces of these rugulosesities white especially towards centre (purple or becoming suffused with purple towards apices of lobes), rest purple-brown, glabrous except at margins of lobes and base of tube; **tube** $\pm$ 1.5 mm long, 3 mm broad, pentagonal, steep-sided alongside stipe of gynostegium, mainly caused by annulus-like thickening of central part of corolla, usually with row of short spike-like and erect papillae near base; **lobes** 10-15 mm long, 5-7 mm broad at base, spreading, narrowly to broadly ovate, acuminate, convex above from

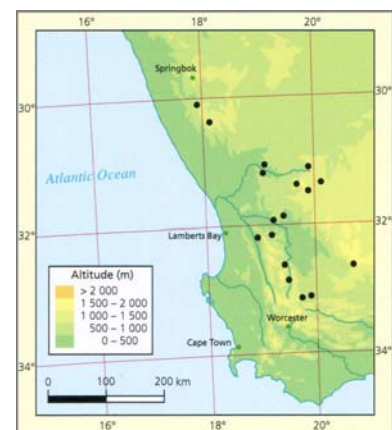


Fig. 15.80. Distribution of *Stapelia arenosa*.

revolute margins adorned with row of short (< 0.5 mm long) white to purple spike-like papillae. **Corona** $\pm$ 3.0-4.5 mm tall, $\pm$ 4-5 mm broad, raised on obtusely pentagonal stipe 1.0-1.5 mm tall, yellow to orange-brown dotted with brown; **outer lobes** $\pm$ 1.5 mm long, spreading $\pm$ at mouth of tube, sparsely pubescent, subquadrate or tapering to truncate emarginate or subacute apex, very slightly channelled down upper surface; **inner lobes** 1.5-3.0 mm long, adpressed to backs of anthers but abruptly recurved near tips of them, dorsiventrally flattened in lower half becoming nearly terete above, narrowly ovate, acuminate, sparsely pubescent, with spreading to ascending laterally flattened triangular to quadrate-emarginate (toothed or crenate) dorsal wing near base.

Distribution and habitat

Stapelia arenosa is fairly widely but sporadically distributed in the Northern Cape and Western Cape. Plants have been recorded from the Kamiesberg near Kamieskroon southwards via the Hantam Mountains, on the drier parts of the escarpment around Nieuwoudtville and on the eastern flank of the Cedarberg to around Karoo Poort in the south-western corner of the Ceres Karoo.

Plants are usually rather scattered and grow both in flat areas under bushes and on stony slopes.

Diagnostic features and relationships

Specimens of *S. arenosa* have a somewhat diffuse habit, usually with few, relatively stout stems. These stems are often irregularly knobby and the tubercles are only partly arranged into rows along them. This is usually due to repeated production of inflorescences on a stem, with new peduncles developing near the tip as the stem elongates and disturbing the arrangement of tubercles into rows.

Flowers are usually produced in small groups near the tip of the stem. The pedicels

remain short and so the flowers are held close to the stem. They open out to be more or less flat, usually with the lobes at least twice as long as broad. The united portion below the lobes varies from being quite prominently thickened and somewhat annulus-like to hardly swollen at all. The inside of the flower is densely covered with irregular, raised, mainly transverse, but also partly reticulated ridges. Towards the centre these ridges are white and slightly translucent so that under a microscope they look a little like a crust of coral or sugar icing. The depressions between them are pale purple-brown. These white ridges become rather more reticulated around the mouth of and inside the small, strongly pentagonal tube but disappear in the tube alongside the stipe of the corona. Towards the middle of the lobes the white on the ridges fades away and the rest of the lobes are purple-brown. There is a row of white or purple, spike-like papillae along the edge of the

lobes but, apart from these, the flower is without hairs. The flowers are odourless, which is rather surprising in view of their dark colour.

In *S. arenosa* the corona is relatively small and predominantly orange, contrasting with the purple-brown and white of the centre of the corolla. The short and almost rectangular outer lobes spread out to touch the corolla beyond the mouth of the tube. They are shallowly channelled above and are usually covered with sweat-like drops of nectar. In some cases windblown dust and sand adheres to these drops and it was this phenomenon which caused Carl Lückhoff to name this species *S. arenosa*. The rather darker inner lobes are tiny (rarely exceeding the anthers) but have larger dorsal horns, often more than one per lobe. Both the inner and outer lobes are 'pubescent' with very fine, white, hair-like papillae.

Although the dimensions of the flowers in *S. acuminata* and *S. arenosa* are similar, the



Fig. 15.81. *S. arenosa*, PVB 7975, northern slopes of Hantam Mountains.

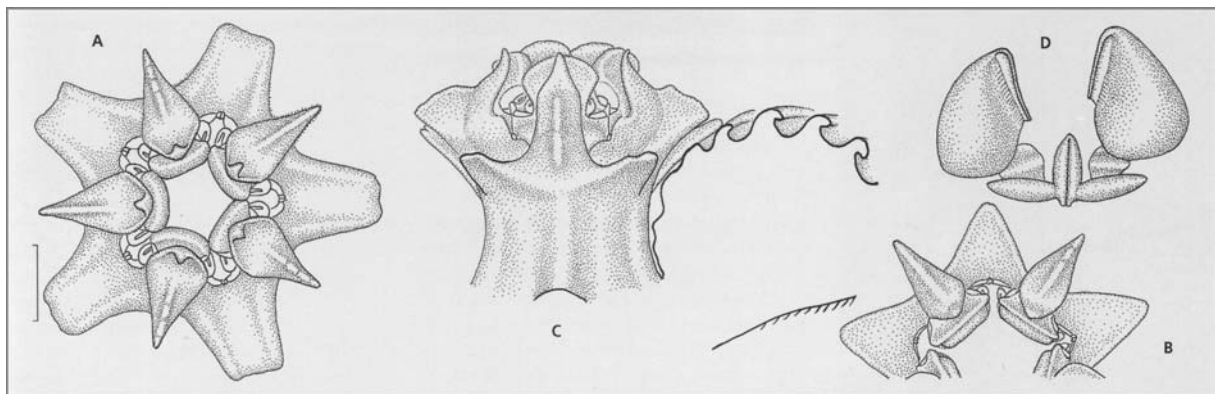


Fig. 15.82. *Stapelia arenosa*. A, B, face view of gynostegium. C, side view of gynostegium and part of centre of corolla. D, pollinarium. Scale bars: A-C, 1 mm (at A); D, 0.25 mm (at A). Drawn from A, D, PVB 3748, Nuwerus, south-eastern Cedarberg; B, C, PVB 7984, north-east of Calvinia.

STAPELIA RUBIGINOSA

surface of the corolla is different and, in the latter, the flowers are also borne apically on the stems. Their respective coronas are also dissimilar, with all the lobes much shorter in *S. arenosa*. *Stapelia arenosa* is closely allied to *S. rubiginosa* and the differences between them are discussed under that species.

History

Stapelia arenosa was first collected before March 1934 in the northern Cedarberg by Joseph Archer, who was the first curator of the Karoo Botanic Garden. Many collections seem to have been made between 1935 and 1937 and some of the material gathered by C. Beukman in 1935 at Botterkloof was described by Lückhoff as *S. arenosa*. Lückhoff described a second species, *S. stultitoides*, in which he found an annulus-like structure around the mouth of the tube and several other differences from *S. arenosa*. Bayer & Frandsen (1975) showed that there was no reasonable basis for upholding two species and that consequently *S. stultitoides* was a synonym of *S. arenosa*.



Fig. 15.83. *S. arenosa*, PVB 3748, Nuwerus, south-eastern Cedarberg.



Fig. 15.84. *S. arenosa*, PVB 6834, north of Nieuwoudtville.

13. *Stapelia rubiginosa*

Stapelia rubiginosa Nel, *Jahrb. Deutschen Kakt.-Ges.* 3: 20 (1935).

Gonostemon rubiginosus (Nel) P.V.Heath, *Calyx* 1: 19 (1992).

Type: South Africa, Richtersveld, Remhoogte, *H. Herre* sub STE 5218 (missing).

Neotype: Richtersveld, Kliphogte, *H. Hall* sub NBG 422/54 (NBG).

Succulent forming diffuse to dense clump up to 300 mm (1 m) diam. **Stems** 60-300 mm long, 10-20 mm thick, decumbent, shortly pubescent, purple-green; **tubercles** widely spaced along stem, not prominent, joined into 4-6 obtuse angles along stem with shallow grooves between them; **leaf-rudiments** 1.0-1.5 mm long, erect, deltoid. **Inflorescences** pubescent, 1-4 per stem mainly in upper half, each of 1-5 flowers developing in gradual succession $\pm$ without peduncle; **pedicel** 3-6 mm long, 1.5 mm thick, spreading, holding flower facing outwards; **sepals** 2.5-3.0 mm long, 1.5-2.0 mm broad at base, deltoid, acute. **Corolla** 20-25 mm diam., reflexed-rotate; outside purplish green with 1-3 darker slightly outstanding veins; inside densely covered with raised transverse broken ridges on lobes becoming less rough and more reticulated on centre around corona, glabrous except for patch of sharp-tipped hairs up to 1 mm long along margins (each arising on papilla) and small papillae near tips of lobes, towards centre red-purple with tips of ridges cream to greenish, on lobes wholly red-purple to dark purple, occasionally whole flower yellowish suffused with red towards edges of lobes; **tube** $\pm$ 1 mm long, 4 mm broad, pentagonal, steeply sided alongside gynostegium and entirely formed by thickening of corolla in centre into raised annulus-like patch; **lobes** 6 mm long, 5-6 mm broad at base, spreading and usually reflexed towards tips, ovate-deltate, acute. **Corona** 2.5-3.0 mm tall, 4-6 mm broad, raised on stout obtusely pentagonal maroon stipe $\pm$ 0.5 mm long, purple-brown; **outer lobes** $\pm$ 2.5 mm long, ascending then spreading with descending apices, $\pm$ deltoid, acute, channelled down middle leading to deeply cupular base beneath guide-rails, covered with short white hairs all over outside and on margins near base, usually wet with secretion on inside; **inner lobes** $\pm$ 1 mm long, adpressed to backs of anthers and usually nearly equalling them, becoming broader towards truncate to emarginate or slightly bilobed apex, dorsiventrally flattened, covered on outside with short white hairs except near apex.

Distribution and habitat

Stapelia rubiginosa is endemic to the Richtersveld on the southern side of the Orange River, in the north-westernmost corner of South Africa. It was originally collected west of the escarpment at Remhoogte and also at Cornell's Kop in 1947. Both of these localities are at altitudes of below 350 m where extreme desertification may have led to this species dying out in the area. More recent collections all seem to have been made at higher altitudes (500-800 m) in the hilly country north-west, north and south of Eksteenfontein.

Plants are usually widely scattered and are

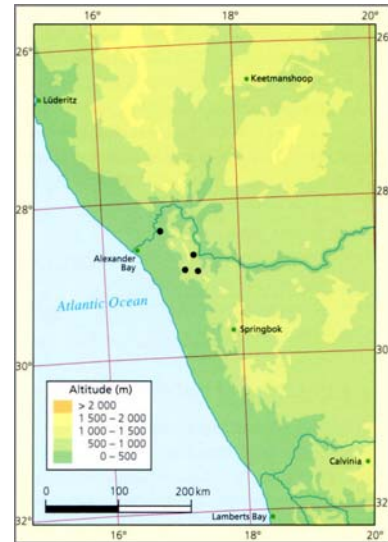


Fig. 15.85. Distribution of *Stapelia rubiginosa*.

mostly found inside bushes on stony, often north-facing slopes, frequently with a wide selection of other succulents.

Diagnostic features and relationships

Exposed specimens of *S. rubiginosa* form dense clumps and may become very large but those that are sheltered often have few stems, which may reach 300 mm long and tend to lean on the surrounding branches for support. The stems are always quite thick and usually around 15 mm in diameter. Towards their bases they are without much of a groove between the angles and so they are almost square in cross-section. In the upper half the angles are often somewhat disorganised by repeated production of inflorescences as the stem elongates.

The relatively small flowers are produced near the tips of the stems in small clusters. They are borne on short pedicels (usually not more than 4 mm long) and, while the lobes do not actually wrap around the stem, they bend backwards towards it, often partly obscuring other buds in the same inflorescence. The interior of the corolla is covered with low, broken, transverse ridges on the lobes. Towards the centre these ridges become flatter and there they are also reticulated rather than only transverse. Most of the flower is dark purple to reddish but towards the middle (below the lobes) the ridges become pale and the centre has an altogether paler appearance than the rest. Yellowish flowers which are suffused with red towards the edges are also known. The area below the lobes is distinctly thickened into an annulus-like cushion and this gives rise to the short, pentagonal tube which surrounds the



Fig. 15.86. *S. rubiginosa*, hort. Russel, Eksteenfontein, with the flowers only faintly rugulose.

base of the gynostegium quite closely. Except for a row of rigid hairs near the margins of the lobes, each of which arises on a papilla, the corolla is glabrous.

The outer corona lobes spread out at the mouth of the tube just above the annulus and superficially they appear to consist of short, deltoid lobes with a groove down the centre. However, dissection reveals that they actually consist of quite a bit more than this and form a deep, quite narrow cup beneath each guide-rail. Their upper surfaces are usually covered above with pools of nectar. The inner lobes are small, becoming broader towards their apices, and they just cover the anthers. They and the outer lobes are covered on the outside with white, hair-like papillae which are longest and most clearly visible on the outer lobes.

The three species *S. arenosa*, *S. rubiginosa* and *S. rufa* all have 'pubescent' coronas

and seem to be closely related as they have similarly coloured rugulose corollas and similar coronas (although this is not supported in the phylogeny assumed here). As Leach (1985) pointed out, *S. rubiginosa* is most closely allied to *S. arenosa* but it differs from it by the shorter and broader corolla lobes and the considerably more thickened annulus. Slightly less obvious differences lie in the deep nectarial cup formed by the outer corona lobes and the short, truncate inner lobes without any trace of a dorsal horn.

History

Stapelia rubiginosa was discovered by Hans Herre at Remhoogte in September 1929. Relatively few collections have been made since then and it remains a rare and little-known species.



Fig. 15.87. *S. rubiginosa*, PVB 8299, south of Eksteenfontein, flower with a particularly pale centre.



Fig. 15.88. *S. rubiginosa*, PVB 8299, south of Eksteenfontein, with the flowers more roughly rugulose.

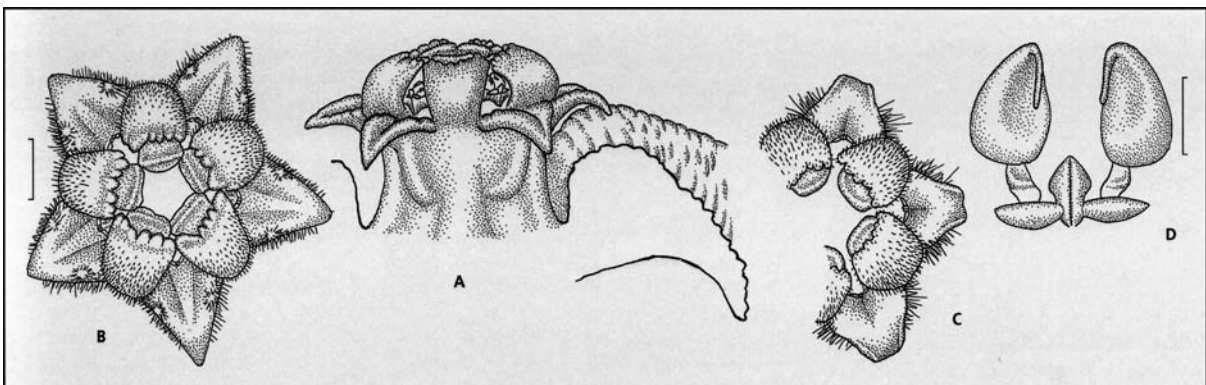


Fig. 15.89. *Stapelia rubiginosa*. A, side view of gynostegium and part of centre of corolla. B, C, face view of gynostegium. D, pollinarium. Scale bars: A-C, 1 mm (at B); D, 0.25 mm. Drawn from A, B, D, hort. E. Aslander; C, PVB, 10 km north of Eksteenfontein.

STAPELIA SURRECTA

14. *Stapelia surrecta*

Stapelia surrecta N.E.Br., Fl. Cap. 4 (1): 970 (1909).
Gonostemon surrectus (N.E.Br.) P.V.Heath, Calyx 1:
 18(1992).

Type: South Africa, Cape, Tanqua Karoo, Marloth
 3791 (missing).

Neotype: Pienaarsfontein, Leach & Bayer 16070
 (PRE, holo.; BOL, K, SRGH, Z, iso.).

Stapelia surrecta var. *primosii* C.A.Lückh. in A.C.
 White & B. Sloane, Stap., ed. 2, 3:1145 (1937).

Gonostemon surrectus var. *primosii* (C.A.Lückh.)
 P.V.Heath, Calyx 3: 8 (1993).

Type: Verlatekloof, near Sutherland (missing).

Lectotype (selected here): White & Sloane, Stap.,
 ed. 2, 2: fig. 436.

Small succulent forming diffuse clump 150-300 mm diam., with few relatively stout stems. **Stems** 50-200 mm long, 8-15 mm thick, decumbent, shortly pubescent, green suffused with purple; **tubercles** 3-5 mm long, widely spaced along stem and obtusely conical, usually joined into 4 obtuse angles (sometimes with groove between them) and then stem $\pm$ square in cross-section; **leaf-rudiments** 1.5-2.5 mm long. **Inflorescences** pubescent, 1-6 per stem mainly near apex, each with 2-8 flowers opening in gradual succession on peduncle gradually lengthening to 10 mm; **pedicel** (12-) 20-35 mm long, 1.5-2.0 mm thick, usually ascending and holding flower facing upwards; **sepals** 3-5 mm long, $\pm$ 1.5 mm broad at base, lanceolate-ovate, acute. **Corolla** 6-15 mm long, 22-40 mm diam., almost rotate to shallowly campanulate; outside pinkish brown with 1-3 prominent (not raised) longitudinal veins on each lobe; inside smooth to finely transversely rugulose, usually pinkish to purplish brown becoming yellowish towards centre, sometimes yellow suffused with brown towards tips, glabrous; **tube** 2-4 mm deep, becoming narrow and distinctly pentagonal lower down around base of gynostegium; **lobes** 9-14 mm long, 6 mm broad at base, ascending to spreading, ovate-acuminate, very slightly convex above with margins slightly reflexed. **Corona** $\pm$ 5 mm tall, $\pm$ 5 mm broad, raised on obtusely pentagonal stipe $\pm$ 1 mm long, red becoming yellow towards base or yellow; **outer lobes** $\pm$ 1.5 mm long, ascending with spreading tips, $\pm$ bifid at apex into deltoid obtuse lobules, concave above; **inner lobes** 3-4

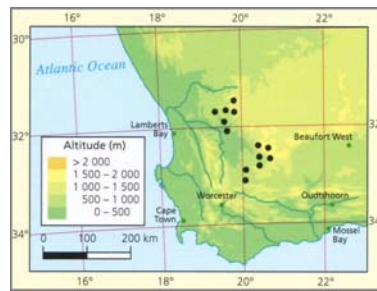


Fig. 15.90. Distribution of *Stapelia surrecta*.

mm long, adpressed to backs of anthers then erect at tips of anthers, connivent then spreading, dorsiventrally flattened in lower half becoming terete above, obtuse, with ascending laterally flattened and narrowly to broadly deltoid dorsal wing 2-4 mm long near base.

Distribution and habitat

Stapelia surrecta is only known from the Ceres Karoo where it is found mainly on the lower slopes of the escarpment and on hills at its base

from a little west of Bloukrans Pass eastwards and southwards to Verlatekloof. It has also been recorded on some dry tillite hills south-east of Karoo Poort. *Stapelia surrecta* is always found on shales or tillites and does not occur at all in the sandstones that form the western boundary of the Ceres Karoo (where *S. arenosa* and *S. hirsuta* grow). Specimens are found under small bushes on stony slopes and are usually quite scattered.

Diagnostic features and relationships

Plants of *S. surrecta* are not distinguishable at all from those of *S. arenosa*, having the same rather diffuse habit and forming similarly lax clumps. Their respective stems are of a similar thickness and colour and in both there are many inflorescences towards the tips of the stems which disrupt the angles.

However, the flowers of *S. surrecta* are quite distinctive. They are usually held on a fairly long pedicel and face upwards. The outside is mainly pinkish brown. Inside the colour varies



Fig. 15.91. *S. surrecta*, PVB 7575, south of Die Bos, Ceres Karoo.

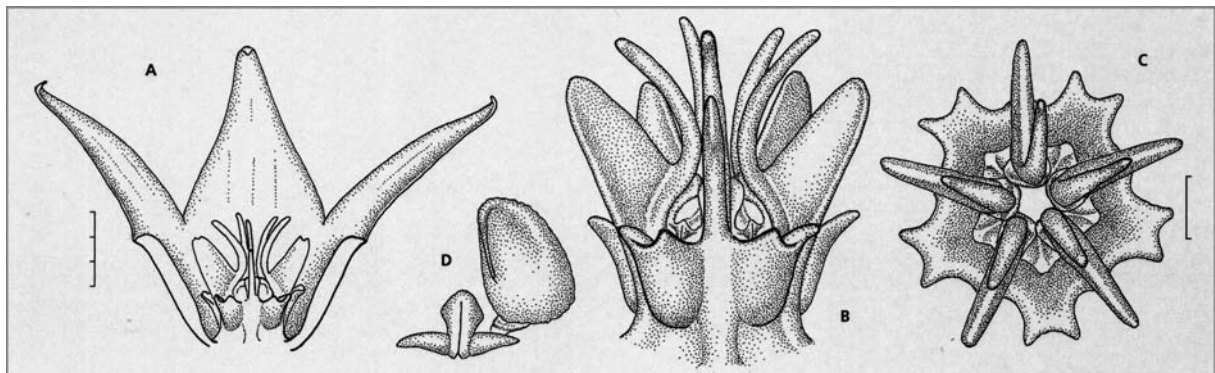


Fig. 15.92. *Stapelia surrecta*. A, side view of dissected corolla. B, side view of gynostegium. C, face view of gynostegium. D, part of pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at C); D, 0.25 mm (at A). Drawn from PVB 2519, south-east of Karooport.



Fig. 15.93. *S. surrecta*, PVB 7575, south of Die Bos, Ceres Karoo.



Fig. 15.94. *S. surrecta*, PVB 5987, east of Koedoeberge, Ceres Karoo, flowers with unusually short corolla lobes.

from pinkish brown, becoming paler and yellowish towards the centre, to yellow suffused with brown towards the tips of the lobes. The inner surface is usually smooth and slightly shiny, only occasionally with fine, irregularly transverse ridges and then mainly towards the tips and the margins of the lobes. There are no hairs anywhere on the inside. The lobes usually spread quite broadly and the united portion below them varies from nearly flat to distinctly funnel-shaped, usually with a strongly pentagonal part around the base of the gynostegium that is accentuated by fold-like grooves running down from the sinuses of the lobes. Some flowers emit a faint, sweet scent.

The corona varies from bright red to pale yellow. Here the outer lobes are very short but are laterally fused lower down to the bases of the inner lobes to form quite a deep cup around the guide-rails, so these rails cannot be seen from the side. The inner lobes rise in the centre and then diverge, usually with relatively long and sometimes quite broad dorsal horns.

In the phylogeny proposed here it is suggested that *S. surrecta* is closely allied to *S. engleriana*, but it is also possible that it is closer to others such as *S. arenosa* or *S. flavopurpurea*.

History

Stapelia surrecta was discovered by Rudolf Marloth somewhere in the Ceres Karoo before 1909 and sent to N.E. Brown at Kew. Somehow no specimen of Marloth's collection came to be preserved, nor is this species mentioned at all in his account of the flora of South Africa (Marloth 1932).

15. *Stapelia engleriana*

Stapelia engleriana Schltr., Bot. Jahrb. Syst. 38: 49, fig. 8 (1905).

Tromotriche engleriana (Schltr.) L.C. Leach, J. S. African Bot. 48: 425 (1982).

Type: South Africa, cultivated material at Berlin-Dahlem (missing).

Neotype: South Africa, Cape, Zout Kloof, N.S. Pillans 60 (BOL).

Small succulent forming clump to 300 mm diam., with some rhizomatous stems. **Stems** 30-300 mm long, 10-22 mm thick, prostrate to ascending above ground, shortly pubescent, grey-green; **tubercles** 2-4 mm long, widely spaced along stem and broadly conical, joined into 4 obscure obtuse angles along stem, stem $\pm$ square in cross-section; **leaf-rudiments** < 1 mm long. **Inflorescences** pubescent, 1-3 randomly distributed along stem, each with 1-3 flowers developing usually in gradual succession on short peduncle (< 5 mm long) with few deltoid bracts < 1 mm long; **pedicel** 10-18 mm long, 2 mm thick, pale green, ascending with spreading apex holding flower facing horizontally; **sepals** 4-6 mm long, 1 mm broad at base, ovate-acuminate. **Corolla** 18-22 mm diam., rotate with lobes folded tightly back under tube to form ring around gynostegium; outside purplish on lobes to cream at base of tube, with 5 prominent (not raised) longitudinal veins on each lobe; inside finely transversely rugulose fading away towards base of tube and beyond middle of lobes, dark purple-brown to red becoming pale yellow spotted with purple-brown in lower half of tube, glabrous except for small short dark hairs (< 0.25 mm long) along edge of lobes near margins and fine acute papillae in tube becoming longer ($\pm$ 0.25 mm) and white in lower half of tube; **tube** $\pm$ 3-5 mm long, 10 mm broad, pentagonal, steep-sided with flat base around stipe, with corolla thickened below bases of lobes; **lobes** 10-12 mm long, 10-12 mm broad at base, tightly reflexed under corolla, ovate-deltate. **Corona** $\pm$ 9.5-10.0 mm tall, $\pm$ 8-11 mm broad, raised on obtusely pentagonal stipe 1.0-1.5 mm long; **outer lobes** 3-4 mm long, 3 mm broad, ascending-spreading, obtusely subquadrate to circular, obtusely bilobed and notched at apex, purple-brown becoming yellow along edges towards base, with margins folded slightly downwards and above slightly channelled towards base; **inner lobes** 5-8 mm long, adpressed to backs of anthers then connivent-erect in column above style-apex and recurved above, dorsiventrally flattened towards base becoming terete above with clavate-tuberculate apex, with ascending laterally flattened linear dorsal horn up to 5 mm long near base, pale yellow streaked with purple-brown.

Distribution and habitat

Stapelia engleriana is widely distributed in the dry parts of the south-western Karoo. There are two known localities on outcrops of tillite in the Worcester-Robertson Karoo. It is of more regular occurrence in the western parts of the Great Karoo from Touws River to Fraserburg, Beaufort West and southwards to Rietbron, and it is also fairly widespread in the Little Karoo. A single record exists from the south-eastern edge of the Ceres Karoo.

Plants usually grow on stony shale or tillite slopes under stones or small bushes, often sheltering under or growing socially with shrubs of *Rhigozum obovatum*.

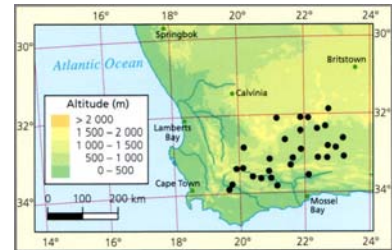


Fig. 15.95. Distribution of *Stapelia engleriana*.

Diagnostic features and relationships

In many places where *S. engleriana* grows, conditions are harsh and the covering bushes are heavily grazed by livestock. Under these circumstances the stems do not exceed 60 mm long. However, when the plants are properly sheltered under bushes or among stones, the stems can reach 300 mm long and form quite dense mats.

This most distinctive *Stapelia* is almost always reliably identifiable even without flowers. The fairly thick, square, prostrate to rhizomatous stems are unlike those of any other stapeliad except *Stapeliopsis saxatilis*. However, *S. engleriana* has obviously pubescent stems and consequently these two are not at all easily confused, even when they occur together.

Florally *S. engleriana* is also unmistakable. The flowers are generally about 20 mm in diameter, with the lobes folded back and pressed tightly against the tube to give it the shape of a turban or a large button. They are noticeably long-lived and remain open for up to eight days, giving off a faint rubber-like, unpleasant odour for the first few days. On the inside of the tube they are mostly quite coarsely transversely rugulose and uniformly dark purple-brown to reddish but sometimes the tips of the ridges on the surface are yellow. The tube is rather deeper than is usual for *Stapelia*.



Fig. 15.96. *S. engleriana*, PVB 3666, east of Beaufort West along road to Aberdeen, showing the oddly shaped bud and the manner in which the corolla lobes are pressed tightly to the back of the tube.

STAPELIA ENGLERIANA

and contains most of the gynostegium. It is very strongly pentagonal, with considerable inward bulges below the lobes (and opposite the outer corona lobes). The sides of the tube are quite obviously thickened (more so than is usual for *Stapelia*) and are usually undercut at the base so that the gynostegium stands in a fairly broad, flat area. This flat area is usually yellow speckled with red and is smooth rather than rugulose. The presence of such a broad base of the tube is also unusual for *Stapelia*, where the lower part of the corolla tube is usually quite close to the pedestal on which the gynostegium stands.

In most stapelias the outer corona lobes are deeply channelled down the upper surface

whereas here the edges are folded downwards and the lobes are convex above. They are also unusually broad. The long and slender inner lobes are terete above, becoming swollen and somewhat tuberculate towards their tips. Their dorsal horns are relatively long and slightly laterally flattened.

A button-shaped flower where the lobes are also strongly folded back is also found in *S. erectiflora* but there the flowers are smaller and very different in structure. Several characters of the corona suggest a relationship with *Tromotriche revoluta* but in fact *S. engleriana* is closer to species of *Stapelia* than to any species in *Tromotriche* (Bruyns 1995a).



Fig. 15.97. *S. engleriana*, PVB 6671, south of Victoria West.



Fig. 15.98. *S. engleriana*, PVB 6671, south of Victoria West, with relatively little red in the flower.

History

The first known collection of *S. engleriana* was made by Joseph Burke, probably around Beaufort West early in 1842. It was described by Rudolf Schlechter from a living plant that he found in the Botanical Garden at Berlin-Dahlem sometime around 1905. He dedicated it to H.G. Adolf Engler, who was the director of the garden and museum at Dahlem for many years and was a well-known figure in German botany during that period. The specimen from which it was described had no data with it and Schlechter thought that it had originated in East Africa and had been sent to the gardens by Stuhlmann. In November 1902, shortly before Schlechter described it, N.S. Pillans collected specimens just north-west of Laingsburg. Subsequently, records have gradually accumulated and today this widely distributed species of the Karoo is reasonably well documented over its range.

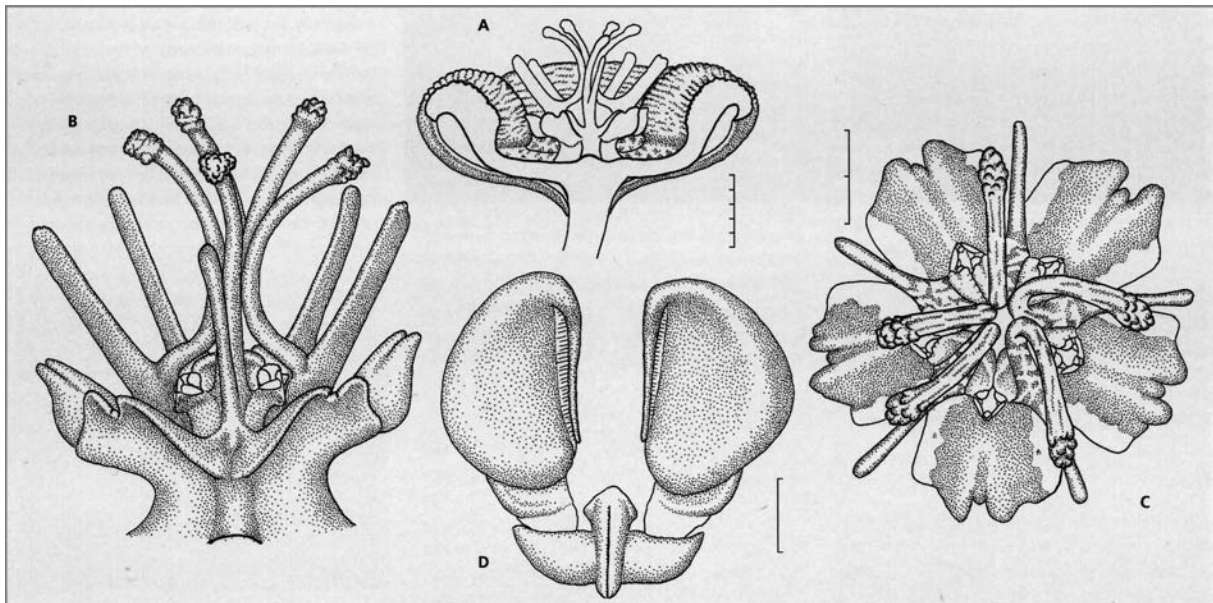


Fig. 15.99. *Stapelia engleriana*. A, side view of dissected flower. B, side view of gynostegium. C, face view of gynostegium. D, pollinarium. Scale bars: A, 5 mm; B, C, 2 mm (at C); D, 0.25 mm. Drawn from: A, PVB 6671, south of Victoria West; B-D, W.R. Branch 320.

16. *Stapelia cedrimontana*

Stapelia cedrimontana Frandsen, *Cact. Succ. J. (US)* 47: 260 (1975).

Type: South Africa, Cape, Buffelshoek Pass, Citrusdal, Frandsen 59 (BOL, holo.; PRE, iso.).
Stapelia montana L.C.Leach, *S. African J. Bot.* 3:175 (1984).

Gonostemon montanus (L.C.Leach) P.V.Heath, *Calyx* 1:19(1992).

Type: Cape Province, Groot Winterhoek Mountains, Bayer 1602 (NBG, holo.; K, MO, PRE, SRGH, iso.).

Stapelia montana var. *grossa* Leach, *S. African J. Bot.* 3:176(1984).

Gonostemon montanus var. *grossus* (L.C.Leach) P.V.Heath, *Calyx* 1:19 (1992).

Type: Cape Province, Witels River, Bruyns 1436 (NBG).

Small succulent forming dense clump, 150-500 mm diam. **Stems** 50-200 mm long, 5-10 mm thick, erect, $\pm$ glabrous, green mottled with purple; **tubercles** 1-3 mm long, widely spaced along stem and obtusely conical, joined into 4 obtuse angles, with stem square to slightly concave-sided in cross-section; **leaf-rudiments** 1.5-2.5 mm long. **Inflorescence** finely pubescent, reddish, 1 (-2) per stem near base, with 1-3 flowers developing in gradual succession on stout peduncle (up to 10 mm long) with few deltoid bracts $\pm$ 1 mm long; **pedicel** 12-35 (-40) mm long, 2 mm thick, spreading with ascending apex holding flower facing horizontally or upwards; **sepals** 5-6 mm long, 1 mm broad at base, lanceolate, acute. **Corolla** 30-50 (-60) mm diam., rotate; outside pale green to reddish usually with 3-5 prominent (not raised) longitudinal veins on each lobe; inside transversely rugulose, pale brown to dark purple-red with cream to yellow on rugosities,

glabrous except for fine pubescence towards apices of lobes and base of tube; **tube** $\pm$ 1.5 mm deep, pentagonal, steep-sided around stipe of gynostegium, corolla thickened around mouth; **lobes** 15-20 mm long, 7-9 mm broad at base, spreading to reflexed, ovate-acuminate, convex above from revolute margins with slender white cilia 2-3 mm long. **Corona** $\pm$ 4.5-6.0 mm tall, $\pm$ 6-10 mm broad, raised on thick pentagonal stipe 1 mm tall, dark purple becoming reddish towards base and on stipe, glabrous; **outer lobes** 3-4 mm long, 1.0-1.5 mm broad, ascending-spreading, oblong, obtuse to truncate or emarginate, apiculate; **inner lobes** 2.5-4.0 mm long, $\pm$ 1 mm broad, adpressed to backs of anthers then erect to connivent and recurved above, dorsiventrally flattened below becoming terete above, narrowly ovate-acuminate, with spreading $\pm$ deltoid laterally flattened dorsal wing near base, 3.5-4.0 mm long and $\pm$ 1 mm broad.

Distribution and habitat

Stapelia cedrimontana is known from the Matsikamma Mountain near Vanrhynsdorp southwards into the Cedarberg to Wuppertal and Algeria as well as further south in these mountains to Citrusdal in the west and the Riet River in the south-east. It is also found south-west of this range in the Piketberg, where it occurs at many different localities, mainly at higher altitudes. Material known previously as *S. montana* is found further south still, from the Groot Winterhoek Mountains near Porterville to the western corner of the Hex River Mountains south of Ceres.

Plants are found in locally arid spots surrounded by fynbos, where they grow in shallow soils on banks of sandstone with other succulents such as species of *Oscularia* and *Crassula* or small bushes. They can be locally very plentiful.

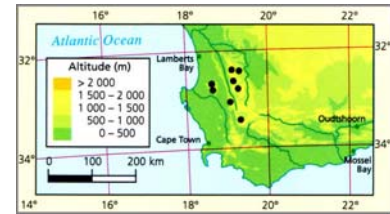


Fig. 15.100. Distribution of *Stapelia cedrimontana*.

Diagnostic features and relationships

Florally *S. cedrimontana* is most distinctive. Flowers are usually about 40 mm in diameter and either flat or with the lobes slightly reflexed. The lobes are fairly narrow, with their margins folded back and there is only a small united area in the centre around the gynostegium. This united area and at least the lower half of the lobes are transversally striped inside with yellow on raised ridges (becoming more or less concentric circles in the centre) against a dark background. However, the extent to which the inside of the corolla is marked with yellow is extremely varied: in some plants these yellow lines are present right to the tips of the lobes and in others they are restricted to the bases of the lobes only. The corolla is largely free of hairs but has long, white cilia along the margins and a few short hairs in the tube.

Plants in the Piketberg have been found to be especially variable, while those from the Cedarberg are less so. Some of them in the Piketberg have smaller flowers with fine hairs on the lobes and these begin to resemble others which have been included in this account in *S. paniculata*.

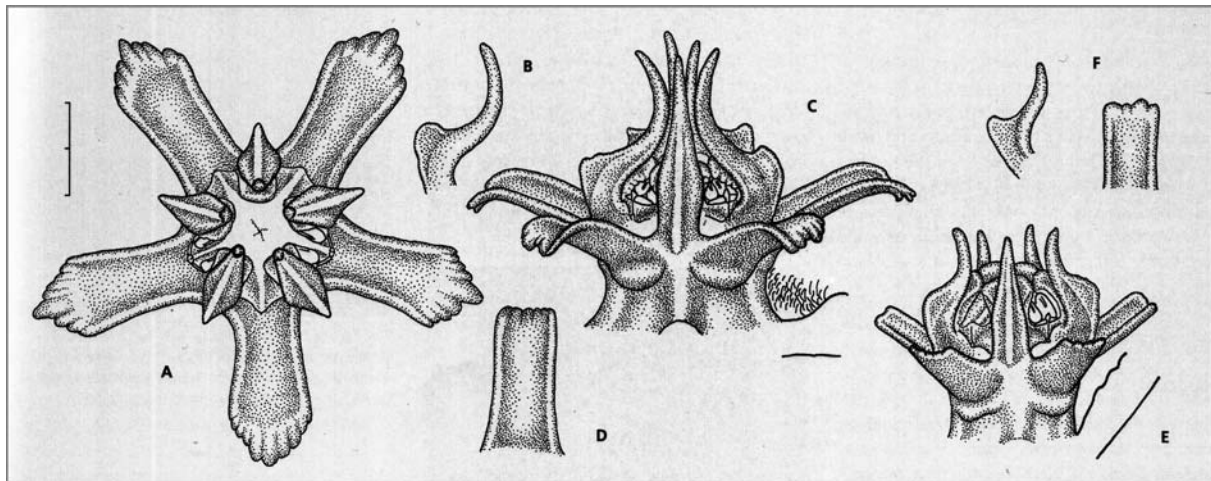


Fig. 15.101. *Stapelia cedrimontana*. A, face view of gynostegium. B, side view of inner corona lobe from A. C, E, side view of gynostegium and small part of centre of corolla. D, face view of outer corona lobe from C. F, inner corona lobe (to left) and outer lobe from other flowers of same collection as E. Scale bars: all 2 mm (at A). Drawn from A, B, PVB 6366, upper slopes of Piketberg; C, D, PVB 7497, western side of Piketberg; E, F, PVB 1437, Witels River.

STAPELIA CEDRIMONTANA



Fig. 15.102. *S. cedrimontana*, PVB 7497, western side of Piketberg.



Fig. 15.103. *S. cedrimontana*, PVB 7497, western side of Piketberg.



Fig. 15.105. *S. cedrimontana*, PVB 6366, upper slopes of Piketberg, in this case with flowers very like those of *S. acuminata*.



Fig. 15.104. *S. cedrimontana*, PVB 6366, upper slopes of Piketberg, flowers with pale markings right to tips of lobes.



Fig. 15.106. *S. cedrimontana*, PVB 6365, Groot Winterhoek Mountains, near Porterville (*S. montana* var. *montana* of Leach).



Fig. 15.107. *S. cedrimontana*, PVB 6365, Groot Winterhoek Mountains.

Leach's *S. montana* is included under *S. cedrimontana*. Although the flowers are often as small as those in *S. paniculata* and therefore somewhat smaller than is typical of *S. cedrimontana*, geographically this taxon is closer to *S. cedrimontana* and occurs just slightly further to the south. Flowers of *S. montana* are exceptionally variable in size and colouring. Many of them have transverse yellow markings inside on a dark background with reflexed lobes which are fairly narrow from the folding back of the margins and these are almost indistinguishable from the flowers of *S. cedrimontana*. Others, where the yellow markings are absent, look less like those of *S. cedrimontana* and more like those of some forms of *S. paniculata*. The stems of *S. montana* are nearly glabrous and, in this respect are more similar to those of *S. cedrimontana* than to those of *S. paniculata*.

plant of hybrid origin and that Brown (1907-09) had almost certainly also misinterpreted Jacquin's figure and included under *S. deflexa* Jacq. several other plants of horticultural origin. As a consequence, plants from the Cedarberg and Piketberg were without a name and, to provide one for them, Frandsen described *S. cedrimontana* in 1975. Plants of this taxon seem to have been recorded for the first time in 1943 by Gerrit Ernst Hendrik Wagener (1891-1944). Wagener farmed at Matjiesrivier in the karroid parts of the central Cedarberg and was encouraged to gather information on succulents which grew in the area by Nortier from Clanwilliam and various botanists from Cape Town (G.N. Wagener, pers. comm. 2000).



Fig. 15.109. *S. cedrimontana*, PVB 1437, Witels River.



Fig. 15.108. *S. cedrimontana*, PVB 1437, Witels River (*S. montana* var. *grossa* of Leach). Here the resemblance to the usual '*cedrimontana*' is clear while it is not so obvious in other specimens from the same place.

History

Plants of *S. cedrimontana* were, for a long time, placed under the name *S. deflexa*, which was described before 1820 by Jacquin from material in cultivation at Schönbrunn gardens in Vienna. Frandsen (1975) and Leach (1985) argued that Jacquin's figure most probably represents a

17. *Stapelia hirsuta*

Stapelia hirsuta L., Sp. PL 1: 217 (1753).

Gonostemon hirsutus (L.) P.V.Heath, *Calyx* 1:17 (1992).

Lectotype: '*S. hirsuta*' in Herb. hort. Cliff. (BM).

Succulent forming dense to diffuse clump 80 mm - 1 m diam. **Stems** 50-300 mm long, 10-20 mm thick, decumbent, shortly pubescent to ± glabrous, uniformly greyish green to green, suffused or mottled with red; **tubercles** 2-4 mm long, widely spaced along stem and obtusely conical, joined into 4 obtuse angles concave between them; **leaf-rudiments** 1-2 mm long. **Inflorescence** pubescent, 1 per stem near base, with 1-3 flowers opening in gradual succession on short stout peduncle (< 5 mm long); **pedicel** 20-70 (-115) mm long, 2-4 mm thick, reddish, spreading, often with ascending apex to hold flower facing upwards on ground or flower facing horizontally; **sepals** 5-13 mm long, lanceolate, attenuate, purplish green. **Corolla** (28-) 50-140 mm diam., rotate; outside purplish cream with 3-7 darker longitudinal veins; inside purple-red with low transverse yellow to cream rugosities fading towards margins and tips of lobes where plain purple-red, sometimes shiny purple-red to purple-black, rugosities also becoming finer towards centre where pale yellow, usually covered towards centre with fine purplish hairs and with patch of longer hairs (up to 12 mm long) each arising on a papilla along margins of lobes, interspersed with small fine hairs, otherwise glabrous; **tube** < 5 mm deep, pentagonal, shallowly bowl-shaped, with corolla very slightly thickened around mouth; **lobes** 15-55 mm long, 8-35 mm broad at base, spreading to reflexed, sub-circular to ovate to ovate-lanceolate, acute. **Corona** 5-16 mm tall, 6-12 mm broad, raised on short obtusely pentagonal stipe 1.0-1.5 mm tall, purple-red becoming yellow towards apices of lobes, glabrous; **outer lobes** 4-6 mm long, ± 2 mm broad at max., ascending to spreading with recurved acute to toothed apex, linear to oblong, deeply channelled down upper surface; **inner lobes** 2.5-12.0 mm long, incumbent on backs of anthers then connivent-erect and erect to strongly recurved, dorsiventrally flattened near base becoming laterally flattened above, with laterally flattened spreading deltoid to lanceolate dorsal wing fused to it at least in lower half.

Stapelia hirsuta is a widespread and extremely variable species. The concept of *S. hirsuta* which was put forward by Leach (1985) already encompassed a very broad range and this has been much extended here to include taxa from Namaqualand and southern Namibia and the Eastern Cape.

Stapelia hirsuta is particularly variable in the pubescence of the stems. In Namaqualand the stems are always finely pubescent. In the south-western Cape almost glabrous stems are found on granites from Malmesbury to Paarl and on sandstone substrates in the Hottentots Holland, Hex River and Langeberg ranges of the Cape Fold mountains. As soon as the shale areas in the Little Karoo are entered, the stems become more pubescent. This is true throughout the Little Karoo, and where sandstone and

shale come close to one another glabrous-stemmed plants (var. *vetula*) may be found growing quite close to ones with pubescent stems (var. *hirsuta*). East of Willowmore all forms of *S. hirsuta* have glabrous stems. In this region they are found mainly on sandstones but also sometimes on shale (e.g. in the former Transkei). Here the common species occurring on shales or dolerite with pubescent stems is *S. grandiflora*.

Stapelia asterias was separated from *S. hirsuta* by the 'densely pubescent, not prominently toothed stems and the characteristic indumentum of the corolla inner surface' (Leach 1985 : 52). From the key on page 9 it appears that the 'characteristic indumentum' refers to the fact that there are 'short weak hairs around the corona, longer and more dense along the sinus radii'. In *S. hirsuta* the flower varies from quite densely hairy in the centre to almost entirely glabrous. In the rather more glabrous flowers the hairs are shorter and confined to an area just around the corona and in five radial patches alternating with the lobes, in other words just as in *S. asterias*.

Leach (1985) considered that 'a close relationship exists between *S. hirsuta* and *S. pulvinata* and there are many similarities, but the numerous important differences leave no doubt regarding the specific distinctiveness of the two taxa, quite apart from their entirely different ecological niches'. The 'numerous important differences' appear to be in *S. pulvinata*

- (1) the single-flowered inflorescence ('most important perhaps')
- (2) the finer, more dense indumentum
- (3) the differently proportional, apiculate, sub-circular corolla lobes
- (4) the much larger inner corona lobes.

On the shales and in *renosterveld* on the western edge of the Little Karoo there is a particularly large-flowered form of *S. hirsuta*. This exhibits most of the characters of *S. pulvinata*, in particular the single-flowered inflorescence, the dense cushion of fine hairs around the centre of the flower and the broadly ovate to sub-circular corolla lobes. In the key of Leach (1985) it works out to be *S. pulvinata* rather than *S. hirsuta*. This therefore completely removes most of the distinctions between the two and I can find no justification for recognising *S. pulvinata* at all.

Leach (1985) separated *S. baylissii*, *S. glabricaulis*, *S. peglerae*, *S. praetermissa* and *S. tsomoensis* on the extent of hairiness of the inside of the corolla: densely hairy on limb and lower part of lobes, glabrous above = *S. glabricaulis*, *S. tsomoensis*; shortly and scantily hairy on the limb, with hairs longer and more dense along the sinus radii = *S. peglerae*, *S. praetermissa*; inner surface glabrous or virtually so, with hairs along edges of lobes and in sinuses = *S. baylissii*.

Stapelia peglerae and *S. praetermissa* were further separated by 'inflorescence from near the base, pedicel 20-40 mm long, corolla up to 75 mm diam., lobes ovate-acuminate' = *S. peglerae*; 'inflorescence randomly disposed, pedicel up to 16 mm long, corolla 30-50 mm diam., lobes narrowly ovate-attenuate' = *S. praetermissa*.

It would appear that, with regard to hairiness of the flower, there is a cline from the one extreme in *S. glabricaulis* to the other in *S. baylissii* and these are not discrete states at all. Once again, there seems to be no point in recognising all these names and, when one finds that, for example, in most specimens of *S. praetermissa* the inflorescences are near the base of the stem, it becomes very difficult to separate these plants under different names.

Another member of this complex is *S. vetula*. Leach (1985) characterised the flowers of this species as 'instantly recognisable by their eciliate, glabrous and usually almost smooth corolla'. He added that the flowers are 'very variable in colour, size and lobe proportions'. Although some flowers of *S. vetula* are entirely without paler markings, in which case they are a rather dull reddish, many of them have thin transverse raised yellow lines on this dull red background. In *S. hirsuta* the inside of the corolla shows a gradation from very hairy to glabrous, sometimes even within a single population. Occasional flowers of *S. hirsuta* are found without cilia (i.e. longer hairs - not the vibratile cilia which are very rare in *Stapelia*) on the margins either (e.g. Leach 1985: fig. 21). The notably non-shiny or matt surface of the flowers of *S. vetula* is, interestingly enough, also found in *S. hirsuta* in those flowers that are without hairs. Leach (1985:63) characterised the stems of *S. vetula* as 'micro-pubescent' and those of *S. hirsuta* as 'pubescent'. In fact, the stems of *S. hirsuta* become more glabrous as one moves further into the sandstones and it is impossible to separate those of *S. hirsuta* at, say, Bain's Kloof or Mitchell's Pass from those of *S. vetula* from north-west of Worcester. In addition, in some plants which one might refer to *S. hirsuta* from this area, the corolla is very nearly (though not entirely) glabrous. There do not appear to be, therefore, two distinct elements in this area.

This brings one to the problem of how to separate *S. vetula* from *S. baylissii* and *S. praetermissa*. In the key (Leach 1985: 6, char. 17) the second two are characterised by 'stems glabrous or virtually so' while *S. vetula* falls under 'stems pubescent or puberulous'. In fact, some stems of *S. hirsuta* can even be as smooth or glabrous as those of *S. baylissii* so, if *S. vetula* is generally more finely pubescent than *S. hirsuta*, this character cannot be relied on to separate *S. baylissii* and *S. vetula* either. *Stapelia baylissii* differs mainly by its rather more rugulose, generally considerably smaller corolla and the

STAPELIA HIRSUTA

relatively few hairs around the margins of the lobes. In view of the extreme variation in the distribution and quantity of hairs in *S. hirsuta*, it is felt that this is not a good character on which to base other closely allied species.

The relationship of *S. hirsuta* to *S. grandiflora* is close and the two are difficult to separate in a key. In very large-flowered forms of *S. hirsuta* the rugulosity of the corolla can be quite shallow, and the inner corona lobes are more erect and are tipped with yellow. These are typical character states for *S. grandiflora* and the size of the flowers (120–140 mm diameter) falls well within the range for *S. grandiflora* as well. Nevertheless, although some plants of *S. hirsuta* have extremely robust stems (up to 20 mm thick), they are never as thick as those of *S. grandiflora*. In *S. grandiflora* the stems mostly have the tubercles fused into narrow wings along the stem with a broad, concave area between them, whereas in *S. hirsuta* the angles are thicker and far more blunt with a much narrower concave area between them. The stems are also mostly less hairy in *S. hirsuta*. In general, the flowers of *S. grandiflora* have very much finer and more obscurely marked rugosities inside the corolla than one finds in *S. hirsuta*.

17a. *Stapelia hirsuta* var. *hirsuta*

Stapelia asterias Masson, *Stap. Nov.*: 14, t.14 (1797).

Gonostemon asterias (Masson) P.V.Heath, *Calyx* 1: 17 (1992).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t.14.

Stapelia pulvinata Masson, *Stap. Nov.*: 13, t.13 (1797).

Gonostemon pulvinatus (Masson) P.V.Heath, *Calyx* 1:17 (1992).

Type: Cape, Kamiesberg, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t.13.

Stapelia sororia Masson, *Stap. Nov.*: 23, t. 39 (1797).

Gonostemon grandiflora var. *sororius* (Masson) P.V.Heath, *Calyx* 3: 7 (1993).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 39.

Stapelia comata Jacq., *Stap.*: t. 49 (1806–19).

Stapelia hirsuta var. *comata* (Jacq.) N.E.Br., *Fl. Cap.* 4(1):938(1909).

Gonostemon hirsutus var. *comatus* (Jacq.) P.V.Heath, *Calyx* 3: 7 (1993). **Lectotype:** Jacq., *Stap.*: t. 49.

Stapelia hamata Jacq., *Stap.*: t. 50 (1806–19).

Lectotype: Jacq., *Stap.*: t. 50.

Stapelia depressa Jacq., *Stap.*: t. 55 (1806–19).

Tridentea depressa (Jacq.) G.Don., *Gen. Hist.* 4:118 (1837–8).

Stapelia patula var. *depressa* (Jacq.) N.E.Br., *Hooker's Icon. PL* 20:1.1914 (1890).

Stapelia hirsuta var. *depressa* (Jacq.) N.E.Br., *Gard. Chron. Ser. 3*, 44:169 (1908).

Gonostemon hirsutus var. *depressus* (Jacq.) P.V.Heath, *Calyx* 3: 7 (1993).

Lectotype: Jacq., *Stap.*: t. 55.

Stapelia patula Willd., *Enum. PL*: 281 (1809).

Stapelia hirsuta var. *patula* (Willd.) N.E.Br., *Fl. Cap.* 4 (1): 937 (1909).

Lectotype (selected here): Jacq., *Stap.*: t. 56.

Stapelia stellaris Haw., *Syn. PL Succ.* 19 (1812).

Type: St. *stellaris* 1812, 1811, 1832'(OXF).

Stapelia lucida DC., *Cat. Pl. horti. Monsp.*: 148–9 (1813).

Stapelia asterias var. *lucida* (DC.) N.E.Br., *Fl. Cap.* 4 (1): 952 (1909).

Gonostemon asterias var. *lucidus* (DC.) P.V.Heath, *Calyx* 3: 8 (1993).

Neotype (selected here): living plants cultivated in greenhouse at Montpellier Bot. Gard., 5 Dec. 1816 (MPU).

Stapelia lanifera Haw., *Suppl. PL Succ.* 8 (1819).

Type: (OXF).

Stapelia hirsuta var. *atra* Lindley, *Bot. Reg.* 9: t. 756 (1823).

Lectotype: Jacq., *Stap.*: t. 52.

Stapelia patentirostris N.E.Br., *Gard. Chron. N.S.* 7:140 (1877).

Lectotype (selected here): *Gard. Chron. N.S.* 7: fig. 21 (1877).

Stapelia unguipetala N.E.Br., *Gard. Chron. N.S.* 7: 334 (1877).

Stapelia hirsuta var. *unguipetala* (N.E.Br.) N.E.Br., *Gard. Chron. Ser. 3*, 44:169 (1908).

Type: cultivated plant of unknown origin (missing).

Stapelia villosa N.E.Br., *Hooker's Icon. PL* 20:t.1911 (1890).

Type: Barkly 28 bis (K).

Stapelia affinis N.E.Br., *Hooker's Icon. PL* 20: t. 1912 (1890).

Stapelia hirsuta var. *affinis* (N.E.Br.) N.E.Br., *Fl. Cap.* 4 (1):937(1909).

Gonostemon hirsutus var. *affinis* (N.E.Br.) P.V.Heath, *Calyx* 3: 7 (1993).

Type: Barkly 16 (K).

Stapelia patula var. *longirostris* N.E.Br., *Hooker's Icon. PL* 20:t.1914 (1890).

Stapelia hirsuta var. *longirostris* (N.E.Br.) N.E.Br., *Fl. Cap.* 4(1): 938 (1909).

Gonostemon hirsutus var. *longirostris* (N.E.Br.) P.V.Heath, *Calyx* 3: 7 (1993).

Type: Barkly 54 (K).

Stapelia hirsuta var. *lutea* N.E.Br., *Fl. Cap.* 4 (1): 937 (1909).

Key to the varieties of *S. hirsuta*

1. Stems ± glabrous 2.
2. Inside of corolla wholly glabrous 17d. var. *vetula*
2. Inside of corolla with fine hairs at least along margins of lobes 3.
3. Inside of corolla lobes purplish, with transverse yellow lines 17b. var. *tsomoensis*
3. Inside of corolla lobes wholly dark red to maroon to purple, without transverse yellow lines 17c. var. *baylissii*
1. Stems finely pubescent 4.
4. Hairs on inside of corolla forming dense central cushion, inner corona lobes uniformly dark purple 17a. var. *hirsuta*
4. Hairs on inside of corolla not forming central cushion, inner corona lobes mottled with purple on yellowish 17e. var. *gariepensis*

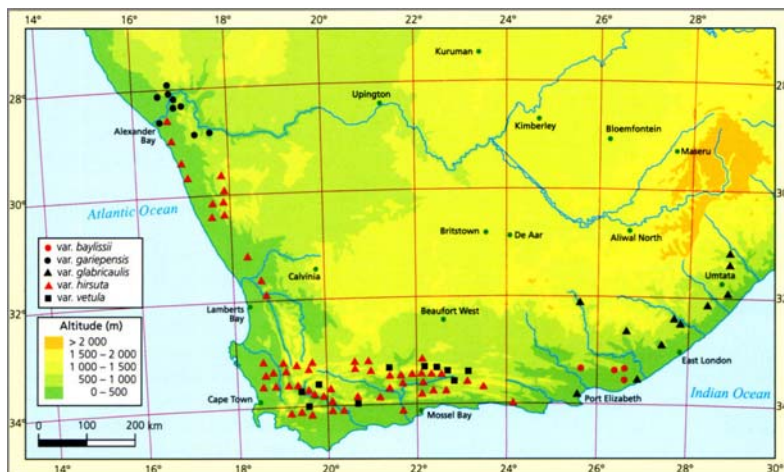


Fig. 15.110. Distribution of *Stapelia hirsuta*.

Gonostemon hirsutus var. *luteus* (N.E.Br.) P.V.Heath, *Calyx* 3: 8 (1993).

Type: Caledon district, near source of Sondereinde R., Piers sub *N.S. Pillans* 618 (BOL).

Stapelia hirsuta var. *grata* N.E.Br., *Fl. Cap.* 4 (1): 938 (1909).

Gonostemon hirsutus var. *gratus* (N.E.Br.) P.V.Heath, *Calyx* 3: 7 (1993).

Lectotype (selected here): near Robertson, *N.S. Pillans* 603 (K).

Stapelia asterias var. *gibba* N.E.Br., *Fl. Cap.* 4 (1): 952 (1909).

Gonostemon asterias var. *gibbus* (N.E.Br.) P.V.Heath, *Calyx* 3: 8 (1993).

Lectotype (selected here): Cape, between Ladismith and Laingsburg, *N.S. Pillans* 607 (BOL).

Stapelia margarita B. Sloane in A.C. White & B. Sloane, *Stap.*, ed. 1:165 (1933).

Stapelia pulvinata f. *margarita* (B. Sloane) G.D. Rowley, *Natl. Cact. Succ. J.* 28: 4 (1973).

Gonostemon X margaritus (A.C.White & B.Sloane) P.V.Heath, *Calyx* 3: 8 (1993) as '*marginatus*'.

Type: sub *White & Sloane* 182 (missing).

Lectotype (selected here): White & Sloane, *Stap.*, ed. 1: fig. 233.

Stems shortly pubescent to $\pm$ glabrous. **Corolla** 50-140 mm diam., $\pm$ rotate; inside usually dull red to purple-black, with faint yellow transverse lines on ruguloseities, sometimes smooth and shiny purple-black all over, densely hairy on united central part and on bases of lobes to nearly glabrous (except towards margins of lobes); **lobes** 25-55 mm long, 15-35 mm broad at base, spreading to reflexed. **Corona:** inner lobes usually uniformly dark purple.



Fig. 15.111. *S. hirsuta* var. *hirsuta*, Mitchell's Pass, in habitat, April 1997.

Distribution and habitat

Var. *hirsuta* occurs in Namaqualand from near the Orange River southwards to around Vanrhynsdorp. In this area it is most common among the western aspects of the gneiss hills of the Kamiesberg from around Springbok to Garies, becoming much more sporadic further south on the edges of the Knersvlakte. Further south again it is found from Malmesbury and Paarl eastwards to the western perimeter of the Little Karoo and further along the edge of the

mountains to Prince Albert. It is also known from dry places on the southern coastal plain from west of Greyton to near Swellendam.

Over its whole range, plants of var. *hirsuta* are found among bushes on gentle slopes or flats or on exposed, rocky outcrops in mountains. In Namaqualand it is sometimes associated with stands of *Galenia africana* in disturbed spots, and on shales in the Little Karoo it frequently shelters among shrubs of *Pteronia incana*.

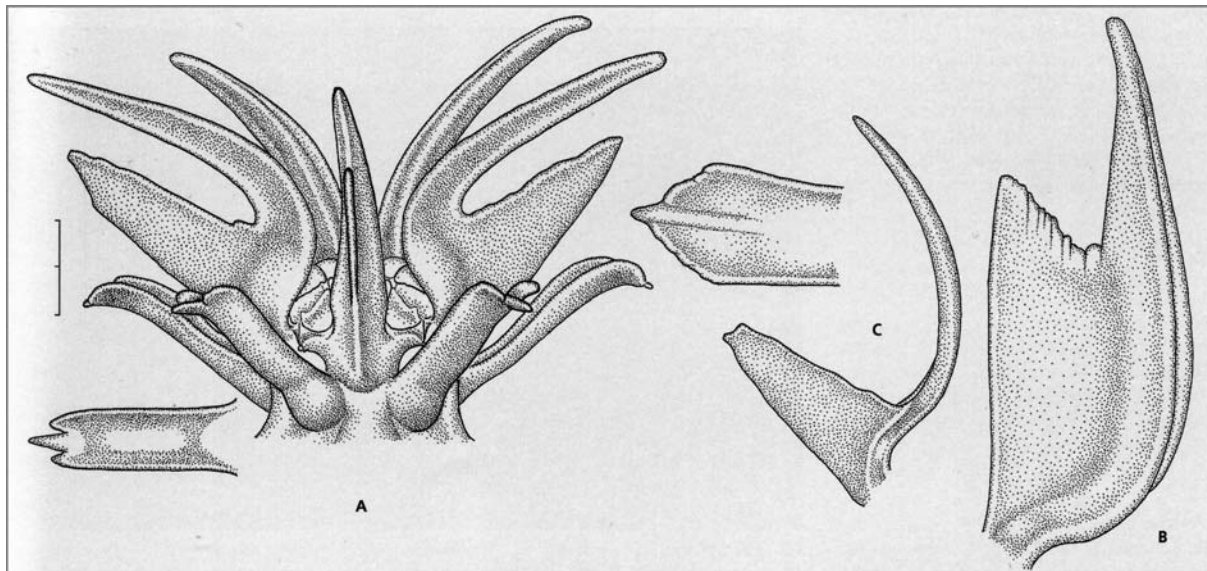


Fig. 15.112. *Stapelia hirsuta* (A, B, var. *hirsuta*; C, var. *vetula*). A, side view of gynostegium (with face view of outer corona lobe alongside). B, side view of inner corona lobe. C, outer corona lobe from above and side view of inner lobe. Scale bars: all 2 mm (at A). Drawn from A, PVB 6980, Nuwekloof, Tulbagh; B, PVB, Hex River Pass; C, PVB 5269, Landsekkloof, Anysberg.

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Fig. 15.113. *S. hirsuta* var. *hirsuta*, Wildeperdehoek Pass, Namaqualand.



Fig. 15.114. *S. hirsuta* var. *hirsuta*, Witberge south-east of Konstel siding.



Fig. 15.115. *S. hirsuta* var. *hirsuta*, Rietvlei No 2, near Montagu.

Diagnostic features and relationships

Like all the varieties of *S. hirsuta*, plants of var. *hirsuta* often become quite large and specimens 300 mm in diameter are not unusual. They form fairly dense clusters of nearly erect, neatly parallel-sided stems which have a shallow, concave area between adjacent angles. Those found on sandstones are sometimes mottled with purple but others are uniformly green.

Var. *hirsuta* is especially variable in the size of the flowers, in their colour and in their degree of hairiness in the south-western Cape and around the western perimeter of the Little Karoo.

These very large-flowered forms from the western edges of the Little Karoo have a dense beard of hairs inside in the centre of the flower, with very broad lobes reflexed behind the flower to emphasise the cushion-like centre. This is similar to most plants in Namaqualand. Further out in the Little Karoo the flowers are smaller, sometimes brightly shiny and more or less uniformly coloured. There are also far fewer hairs inside and these are mainly distributed around the edges of the flower. On sandstone mountains the flowers may also be smaller and are sometimes nearly glabrous.

The follicles in var. *hirsuta* are usually mottled with fine purplish lines on a pale green background.

History

Stapelia hirsuta was, after *Orbea variegata*, the second stapeliad to become known in Europe. White & Sloane (1937) aver that it was first mentioned in Leonard Plukenet's *Almagestum botanicum* of 1696 but it is only clear that *O. variegata* is referred to there. The first figure of it appeared in Johannes Burman's *Rariorum Africanarum Plantarum* of 1738-9. In Linnaeus' *Genera Plantarum* of 1737 there is no clear reference to it either, but in *Hortus Cliffortianus*, which appeared later in 1737, a species with pubescent stems is listed and this is probably *S. hirsuta*. In Linnaeus' *Species Plantarum* of 1753, *S. hirsuta* and *S. variegata* are the only stapeliads listed. It is not known who brought these early



Fig. 15.116. *S. hirsuta* var. *hirsuta*, Bain's Kloof Pass, in habitat, April 1994.



Fig. 15.117. *S. hirsuta* var. *hirsuta*, PVB 7082, Saptou.



Fig. 15.118. *S. hirsuta* var. *hirsuta*, PVB 7082, Saptou, Long Kloof.



Fig. 15.119. *S. hirsuta* var. *hirsuta*, PVB 4568, foot of northern slopes of Anyberg, plant with the shiny corolla typical of '*S. asterias*'.



Fig. 15.120. *S. hirsuta* var. *hirsuta*, Mitchell's Pass, in habitat, April 1994, with flowers almost completely hairless.

specimens of var. *hirsuta* to Europe but since it is fairly common relatively close to Cape Town, its early discovery is not surprising.

17b. *Stapelia hirsuta* var. *tsomoensis*

Stapelia hirsuta var. *tsomoensis* (N.E.Br.)

Bruyns, *comb. et stat. nov.*

Stapelia tsomoensis N.E.Br., *Gard. Chron.* N.S. 18: 168 (1882).

Gonostemon tsomoensis (N.E.Br.) P.V.Heath, *Calyx* 1:17 (1992).

Type: South Africa, Transkei, Tsomo, *Barkly* 32 (K).

Stapelia glabricaulis N.E.Br., *Hooker's Icon. PL* 20: t.1917 (1890).

Gonostemon glabricaulis (N.E.Br.) P.V.Heath, *Calyx* 1:17 (1992).

Type: Cape, Fort Beaufort Division, Blinkwater, *Barkly* 52 (K).

Stapelia peglerae N.E.Br., *Fl. Cap.* 4 (1): 953 (1909)

Gonostemon peglerae (N.E.Br.) P.V.Heath, *Calyx* 1:17 (1992).

Type: Transkei, Mquanduli, *Pegler* 760 (K).

Stapelia forcipis E.Phillips & Letty, *Fl. Pl. South Africa* 12: t. 460 (1932).

Gonostemon glabricaulis var. *forcipis* (E.Phillips & Letty) P.V.Heath, *Calyx* 3: 8 (1993).

Type: locality unknown, Viljoen sub *PRE* 11590 (PRE).

Stems $\pm$ glabrous. **Corolla** 40-75 mm diam., $\pm$ rotate; inside yellowish purple on central part becoming purplish to purple-brown usually with transverse yellow lines on lobes to uniformly pinkish purple, with long hairs on central part and lower parts of lobes as well as their margins; **lobes** 15-30 mm long, 12-20 mm broad at base, spreading to reflexed. **Corona: inner lobes** uniformly dark purple.

Distribution and habitat

Var. *tsomoensis* occupies the easternmost portion of the distribution of *S. hirsuta*. It is not uncommon around the gorge of the Kei River but is generally of very sporadic occurrence from near Queenstown in the south-west to the gorge of the Tsitsa River north of Umtata in the former Transkei.

Plants of var. *tsomoensis* grow among rocks in rather exposed spots, occasionally with short grasses but often with almost no other vegetation.

Diagnostic features and relationships

In var. *tsomoensis*, the stems are uniformly dull grey-green. Although not shiny at all, they are quite glabrous to the touch and the usual papillae that cause them to be pubescent on most other taxa are restricted to small patches around and on the leaf-rudiments. The inflorescence is usually pubescent and the outside of the flower is scantily and finely pubescent.

The inside of the flower may be a dull pinkish brown to purple with relatively few transverse rugosities, mainly on the lobes, or it may be pinkish purple and slightly shiny with fine



Fig. 15.121. *S. hirsuta* var. *tsomoensis*, PVB 5387, Kei River east of Stutterheim.

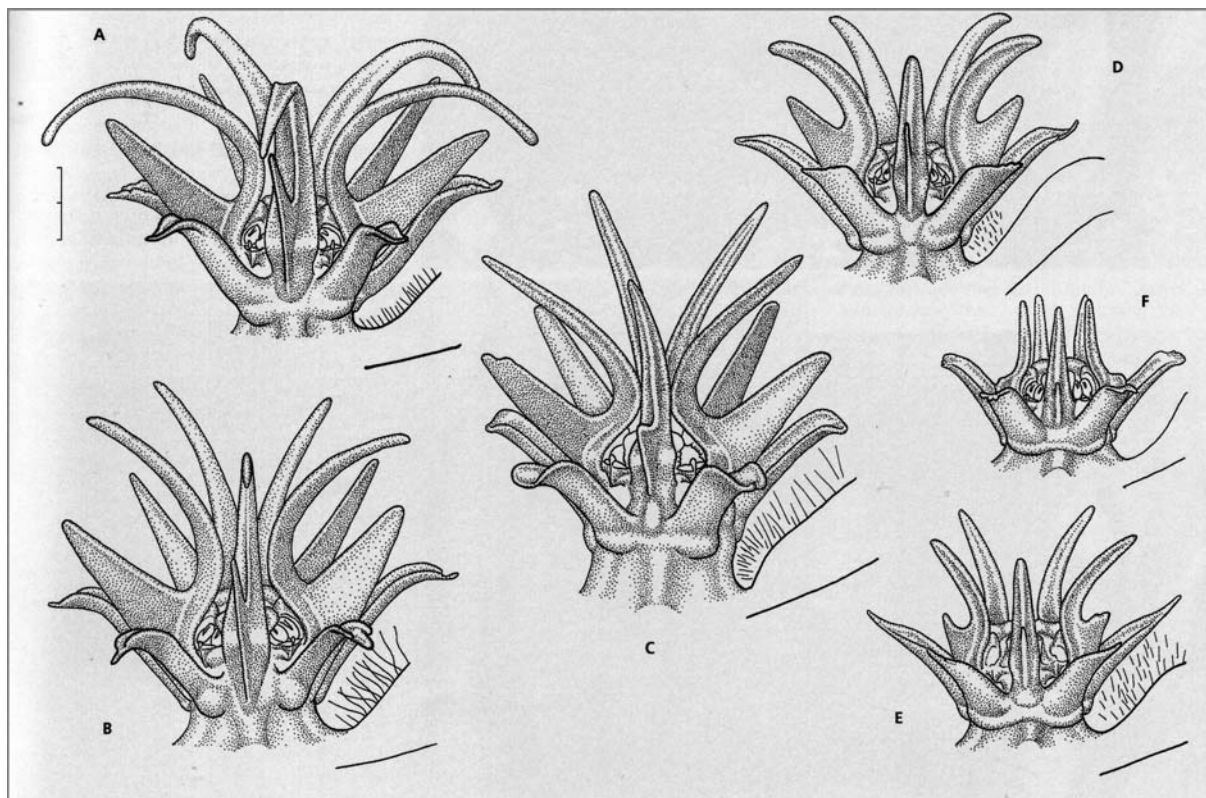


Fig. 15.122. *Stapelia hirsuta* (A-C, var. *tsomoensis*; D-F, var. *baylissii*). A-F, side view of gynostegium. Scale bars: all 2 mm (at A). Drawn from A, B, PVB 2143, Bolo River, north-east of Stutterheim ('*tsomoensis*'); C, PVB 4390, Tsitsa River, north of Umtata ('*peglerae*'); D, PVB 5008, Suurberg Pass, north-west of Grahamstown ('*baylissii*'); E, PVB 7027, Kariega River, south of Grahamstown ('*praetermissa*'); F, PVB 7479, Kariega River ('*praetermissa*').

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transverse rugosities over most of the surface (as in the former *S. peglerae*). Hairs are usually concentrated along the edges (each arising on a papilla and up to 6-7 mm long) and in a fairly



Fig. 15.123. *S. hirsuta* var. *tsomoensis*, PVB 4390, Tsitsa River, north of Umtata, plant belonging to what was formerly called *S. peglerae*.



Fig. 15.124. *S. hirsuta* var. *tsomoensis*, PVB 2143, Bolo River, north-east of Stutterheim.



Fig. 15.125. *S. hirsuta* var. *tsomoensis*, PVB 2143, Bolo River, north-east of Stutterheim.

dense patch near the bases of the lobes, on the flat central area around the corona and into the small tube around its base.

The corona is always purple-brown with slightly paler inner lobes but structurally it is the same as in var. *hirsuta* from much further west.

The follicles in var. *tsomoensis* are always uniformly coloured, without any darker longitudinal stripes.

History

Var. *tsomoensis* was collected in various places in about 1870 and sent to Kew by Henry Barkly. It has remained very little known and few collections have been made since that time.

17c. *Stapelia hirsuta* var. *baylissii*

Stapelia hirsuta var. *baylissii* (L.C.Leach) Bruyns, *comb. et stat. nov.*

Stapelia baylissii L.C.Leach, *S. African J. Bot.* 3:172 (1984).

Gonostemon baylissii (L.C.Leach) P.V.Heath, *Calyx* 1:18(1992).

Type: South Africa, Cape, Suurberg, Round Hill, Bayliss 2786 (PRE, holo.; K, NBG, iso.).

Stapelia praetermissa L.C.Leach, *S. African J. Bot.* 3:171 (1984).

Gonostemon praetermissus (L.C.Leach) P.V.Heath, *Calyx* 1:17 (1992).

Type: Cape Province, Southwell, Leach & Bayliss 15651 (PRE, holo.; K, MO, Z, iso.).

Stapelia praetermissa var. *luteola* L.C.Leach, *S. African J. Bot.* 3:172 (1984).

Gonostemon praetermissus var. *luteolus* (L.C.Leach) P.V.Heath, *Calyx* 1:18 (1992).

Type: Cape Province, Vaalviei, *Stayner* sub KGW 272/70 (NBG).

Stems ± glabrous. **Corolla** 30-60 mm diam., ± rotate; inside ± smooth towards centre becoming prominently transversely rugulose around middle of lobes or all smooth, dark red to maroon to purple and dull to shiny, glabrous except for fine pubescence towards apex of lobes and purple to white hairs ± 1 mm long in narrow strip near and along margins of lobes; **lobes** 15-22 mm long, 8-10 mm broad at base, spreading with recurved tips, ovate-lanceolate. **Corona:** *inner lobes* uniformly dark purple.

Distribution and habitat

Var. *baylissii* is found in the higher areas of the Suurberg, along the Suurberg Pass and on steep spots along the upper reaches of the Witrivier. The forms described as *S. praetermissa* are found south of Grahamstown along the Kariega River.

Plants invariably grow on dry, rocky outcrops, in many cases in the locally semi-arid spots just above and behind cliffs overlooking a river. Most of these areas are surrounded by more dense riverine bush or by *fynbos*.

Diagnostic features and relationships

In var. *baylissii* the stems are dull grey-green and are more or less smooth. The relatively small flowers are dark red to purple inside, with a dull surface in plants from the Suurberg and a shiny surface in plants from along the Kariega River. The inside is often markedly rugulose but may also be nearly smooth. There are usually relatively few hairs - there is usually a patch of them towards the edge of the lobes, occasionally a few in patches adjacent to and below the bases of the lobes and some towards the base of the tube.

The corona lobes in var. *baylissii* are generally much smaller than in most other

forms of *S. hirsuta* and range from structures easily matched in var. *tsomoensis* to ones with smaller outer lobes and very short, erect and not at all recurved inner lobes with only very small dorsal ridges rather than the spreading dorsal fin that is usually present. These much reduced structures are found in the smallest flowers, which have been observed along the Kariëga River, and there is some suggestion here of links with *S. paniculata*.

Stapelia baylissii was characterised (Leach 1985) by its 'heavily rugulose' corolla. However, even in plants from the Suurberg Pass many of them have a quite smooth centre and the rugulosity only begin around the middle of the lobes and continue from there to their apices. Leach (1985) maintained that *S. baylissii* differed from *S. praetermissa* by the 'stouter stems, a basally positioned inflorescence, shorter sepals but larger flowers, with a glabrous corolla surface and proportionally wider, heavily rugulose, strongly convex lobes'.

Two collections have recently been made along the Kariëga River (PVB 7027, PVB 7479). In both of them the stems were 8-22 mm thick (in this respect they were similar to those of *S. baylissii*, where they were given as ± 15 mm thick); the inflorescences were near the bases of the stems; the flowers were between 40 and 45 mm across (i.e. well within the 30-60 mm given by Leach for *S. baylissii*); the inside of the flower had very few hairs (in one hairs were present only at the base of the lobes and in the other they arose in lines running from the bases of the lobes towards the centre); one was smooth inside and the other slightly rugulose; and the lobes were convex for most of their length. *Stapelia baylissii* is itself rather more

variable than Leach suggested. Inflorescences may be produced at any height along the stems (though they appear mainly below the middle), the flowers are sometimes heavily rugulose (as in his fig. 40) but they may have a smooth centre and then may be rugulose only towards the tips of the lobes. Therefore *S. praetermissa* is reduced to synonymy under var. *baylissii*. The follicles of var. *baylissii* are, like those in var. *tsomoensis*, always uniformly coloured, without any darker longitudinal stripes.

History

Material of var. *baylissii* was first gathered before 1947 by Northover, south of Grahamstown and recollected by Roy D.A. Bayliss in about 1965 in the Suurberg Pass to the north of Grahamstown. A yellow-flowered plant was collected by Frank Stayner in 1970 (which was named *S. praetermissa* var. *luteola*) but this has not been found again.



Fig. 15.126. *S. hirsuta* var. *baylissii*, PVB 7479, Kariëga River, south of Grahamstown.



Fig. 15.127. *S. hirsuta* var. *baylissii*, PVB 5008, Suurberg Pass, west of Grahamstown.

17d. *Stapelia hirsuta* var. *vetula*

Stapelia hirsuta var. *vetula* (Masson) Bruyns, *comb. et stat. nov.*

Stapelia vetula Masson, Stap. Nov.: 15, t.16 (1797).

Tridentea ? vetula (Masson) Haw., *Syn. Pl. Succ.*: 35 (1812).

Gonostemon vetulus (Masson) P.V.Heath, *Calyx* 1: 18 (1992).

Type: South Africa, Cape, Hex River Mountains, Masson, Hort. Bayfield. 18/3 (K, *fide* N.E. Brown).

Stapelia juvenula Jacq., Stap.: t. 28 (1806-19).

Tridentea juvenula (Jacq.) Sweet, *Hort. Brit.*, ed. 1:277(1826).

Stapelia vetula var. *juvenula* (Jacq.) A.Berger, Stap. u. Klein.: 282 (1910).

Lectotype: Jacq., Stap.: t. 28.

Tridentea ? simsii Haw., *Syn. Pl. Succ.*: 36 (1812).

Stapelia simsii (Haw.) Schult. in Roem. & Schult., *Syst. Veg.*: 33 (1820).

Stapelia vetula var. *simsii* (Haw.) N.E.Br., *Fl. Cap.* 4(1):964(1909).

Type: missing.

Stapelia nudiflora Pillans, *S. Afr. Garden. & Country Life* 18: 62 (1928, special reprint).

Type: South Africa, Cape, Tradouw Pass, Compton & Cook sub NBG 1967/23 (BOL).

Stems $\pm$ glabrous. **Corolla** 30-80 mm diam., $\pm$ rotate; inside obscurely transversely rugulose, dull (rarely shiny) red to purple-black often with faint yellow transverse lines on rugulosity, glabrous; **lobes** 15-20 mm long, 10-12 mm broad at base, spreading, ovate-acute, flat above. **Corona:** **inner lobes** uniformly dark purple.

Distribution and habitat

Var. *vetula* has been found widely in the sandstone mountains of the Cape Fold System. It is known along the northern slopes of the Hex River Mountains and the Swartberg from north-west of Worcester to Meiringspoort. It has also been recorded on the Anysberg and on the Kamanassie Mountains within the Little Karoo, further south in the Langeberg (e.g. Tradouw Pass) and in the Riviersonderend Mountains.

Plants grow in dry areas within these mountains on locally arid rock outcrops and, although they may be found occasionally on open slopes, they are more common in kloofs which, if they face in the right direction, can be much drier than the surrounding areas. Such locally arid spots often harbour patches dominated by a wide variety of succulents but are usually surrounded by fynbos.

Diagnostic features and relationships

The stems of var. *vetula* are always glabrous to the naked eye but actually they have a fine, sandpapery texture and are quite rough to the

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Fig. 15.128. *S. hirsuta* var. *vetula*, PVB 1701, Jan Du Toit's Kloof, north-west of Worcester, in habitat, March 1978.

touch. Some of them can be attractively mottled with purple-brown on green.

In var. *vetula* the flower is reddish inside, mostly with an unusually dull surface, though shiny-flowered plants do occur, mainly towards the west. The inner surface of the corolla is faintly rugulose and also (again mainly in the west) may be vaguely transversely lined with yellow, mainly on the lobes. It is entirely without hairs.

The corona is typical for *S. hirsuta* but the lack of hairs makes it somewhat more obvious in the centre of the flower than is usually the

case in var. *hirsuta* and the yellow colour towards the bases of the corona lobes is usually quite striking.

The follicles in var. *vetula* are usually mottled with fine purplish lines on a pale green background.

History

Var. *vetula* was first collected by Francis Masson in the mountains around the Hex River Valley, possibly as early as mid-December 1774, when he passed through this area in the company of Thunberg.



Fig. 15.129. *S. hirsuta* var. *vetula*, PVB 5269, Landsekkloof, Anyenberg.



Fig. 15.130. *S. hirsuta* var. *vetula*, PVB 7142, Sanddriftkloof, north of Worcester.



Fig. 15.131. *S. hirsuta* var. *vetula*, PVB 1701, Jan Du Toit's Kloof, north-west of Worcester, in habitat, March 1978.

17e. *Stapelia hirsuta* var. *gariensis*

Stapelia hirsuta var. *gariensis* (Pillans) Bruyns, *comb. et stat. nov.*

Stapelia gariensis Pillans, *S. African Gard. & Country Life* 18: 62 (1928, special reprint). *Gonostemon gariensis* (Pillans) P.V.Heath, *Calyx* 1: 17 (1992).

Type: Cape, Richtersveld, Grootderm, N.S. Pillans 5771 (BOL).

Stapelia johani-lavrani J.J.Halda, *Acta Mus. Richnov. Sect. Natur.* 5: 42 (1998).

Type: Namibia, near Rosh Pinah, Halda 9708416 (?).

Stems very shortly pubescent. **Corolla** 50-100 mm diam., $\pm$ rotate; inside usually shiny red-purple sometimes obscurely lined with yellow, covered densely on united central part and lobe margins with long soft hairs; **lobes** 25-45 mm long, 15-20 mm broad at base, spreading to recurved. **Corona:** *inner lobes* mottled with purple on yellowish.

Distribution and habitat

Var. *gariensis* is known along the lower reaches of the Orange River, where it occurs in the south-western corner of Namibia and in the adjacent parts of South Africa. In South Africa it has been gathered over a somewhat wider area than in Namibia and it is known from the coastal flats a little to the east of Alexander Bay as far as the higher mountains at Hellskloof in the Richtersveld. In Namibia records exist from the Schakalsberg in the southern Namib Desert, from Lorelei and from Namuskluft and Numeis near Rosh Pinah. It has also been observed in some of the deep valleys which lie east of Lorelei and run in a north-south direction towards the Orange River.

Plants are found among rocks or in flat, loamy areas. They occasionally grow entirely in the open or they may shelter under bushes. In both Namibia and South Africa collections have been made at altitudes ranging between 50 and 800 m (up to 1 400 m near Numeisspitze in Namibia), though generally var. *gariensis* is more common at lower altitudes than higher up.

Diagnostic features and relationships

The stems in var. *gariensis* may have a more spreading habit than is usual in *S. hirsuta* and then they can form particularly loose clumps. They are often quite dark purplish green.

The corolla in var. *gariensis* is most similar to that in what used to be called *S. asterias*, from the Little Karoo. It is relatively large, reddish purple and transversely rugulose but only rarely lined with yellow. There is a dense row of hairs along the margins of the lobes and in the centre, spreading to the bases of the lobes.

The follicles in var. *gariensis* are usually mottled with fine purplish lines on a pale green background.

History

Var. *gariensis* was described by N.S. Pillans from material that he gathered in October 1926 at the northern base of the low hills facing the Orange River near Grootderm, during his famous expedition to the Richtersveld. These flowered in his garden in April 1927. Huber (1967) considered this 'species' to be a north-

ern race of *S. hirsuta* and there seems to be no reason to doubt his conclusion. Leach (1985) mentioned the more deeply lobed corolla, the proportionally narrower corolla lobes and the differently shaped buds and related it to *S. asterias*. However, these are all very vague differentia in which there is no evidence at all of discontinuities on which a species could be separated.



Fig. 15.132. *S. hirsuta* var. *gariensis*, PVB 2772, east of Rosh Pinah, Namibia, in habitat, September 1987.

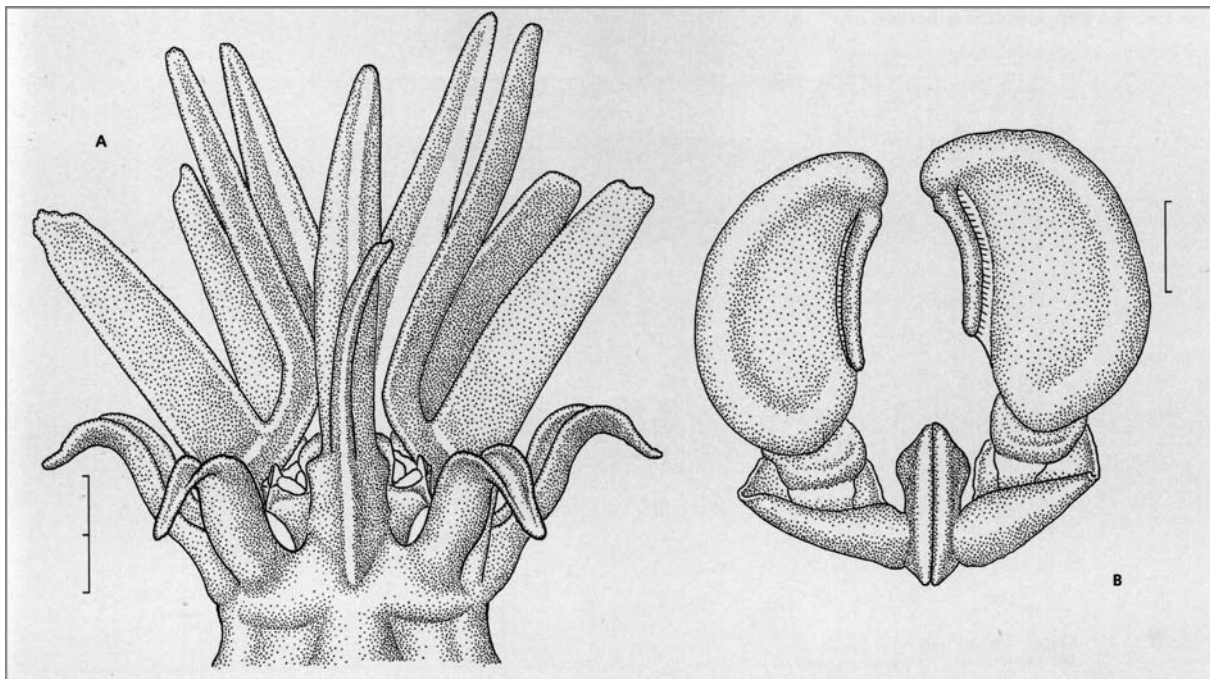


Fig. 15.133. *Stapelia hirsuta* var. *gariensis*. A, side view of gynostegium. B, pollinarium. Scale bars: A, 2 mm; B, 0.25 mm. Drawn from PVB 3048, Lorelei, Namibia.

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18. *Stapelia obducta*

Stapelia obducta L.C.Leach, S. African J. Bot. 3: 169 (1984).

Gonostemon obductus (L.C.Leach) P.V.Heath, *Calyx* 1:17(1992).

Type: Cape, Groot Winterhoek Mountains, Mullens 78 (PRE, holo.; NBG, iso.).

Succulent forming dense to diffuse clump 80-450 mm diam. **Stems** 50-300 mm long, 10-20 mm thick, decumbent, $\pm$ glabrous, green sometimes mottled with red; **tubercles** 2-4 mm long, widely spaced along stem and obtusely conical, joined into 4 obtuse angles (concave between them); **leaf-rudiments** 1-2 mm long. **Inflorescence** finely pubescent, 1 per stem near base, with 1-3 flowers opening in gradual succession on short stout peduncle (5-15 mm long); **pedicel** 15-60 mm long, 2-4 mm thick, reddish, spreading with flower facing horizontally or slightly upwards; **sepals** 8-13 mm long, lanceolate, attenuate, purplish green. **Corolla** 28-35 mm diam. (50-70 mm if lobes spread out), $\pm$ turban-shaped; outside purplish cream with 3-7 darker longitudinal veins; inside purple-red (brown) over whole surface or with few transverse yellow lines on lobes, covered all over with fine purple-red (brown) hairs somewhat longer and denser towards margins; **tube** < 5 mm deep, pentagonal, shallowly bowl-shaped, with corolla very slightly thickened around mouth; **lobes** 16-25 mm long, 15-19 mm broad at base, ovate, acute, strongly folded back behind corolla. **Corona** 9-10 mm tall, $\pm$ 12 mm broad, raised on short obtusely pentagonal stipe 1.0-1.5 mm tall, purple-red becoming yellow towards apices of lobes, glabrous; **outer lobes** 4-6 mm long, $\pm$ 2 mm broad at max., ascending to spreading with recurved acute to toothed apex, oblong, deeply channelled down upper surface; **inner lobes** $\pm$ 6 mm long, incumbent on backs of anthers then con-

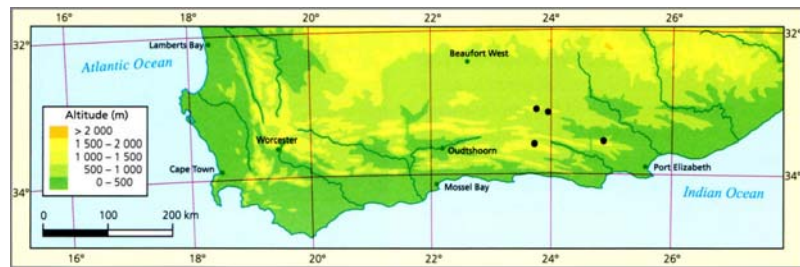


Fig. 15.134. Distribution of *Stapelia obducta*.

nivent-erect and erect to slightly recurved towards tips, dorsiventrally flattened near base becoming laterally flattened above, uniformly dark purple or suffused with yellow towards tips, sometimes with laterally flattened spreading deltoid dorsal wing fused to it at least in lower half.

Distribution and habitat

Stapelia obducta is known from the vicinity of the Cockscomb Peak in the Groot Winterhoek Mountains south of Steytlerville. In this area my own collections have revealed it growing sporadically on steep slopes in a deep gully alongside the peak. I have also *Stapelia obducta* at three separate spots in the Grootrivier Mountains, both west and east of the small railway siding of Fullarton, north-east of Willowmore. Even more interesting is the discovery by George Delpierre of similar plants in the Long Kloof near Joubertina.

Plants of *S. obducta* grow on steep slopes well within the sandstone mountains and have proved to be locally quite plentiful on several occasions. They occur in arid patches sur-

rounded by *fynbos*, among rocks and bushes with a wealth of other succulents such as *Quaqua pillansii*, *Senecio ficoides*, *Cotyledon woodii* and several species of *Adromischus*, *Crassula*, *Gasteria* and *Haworthia*.

Diagnostic features and relationships

In *S. obducta* the stems are more or less glabrous, with a distinctly sandpapery texture. They are pale to bright green and often quite boldly mottled with red.

When the flowers open, the lobes almost immediately fold right back behind the corolla so that it resembles a flattened, furry ball, rather like a turban. This appears to be most distinctive but, oddly enough, in both his discussions of *S. obducta*, Leach (1984a, 1985) did not mention the curious shape of the flower. One can only speculate that, since he knew it from just one single plant, he may have considered this shape to be an aberration.

Leach related *S. obducta* to *S. tsomoensis*

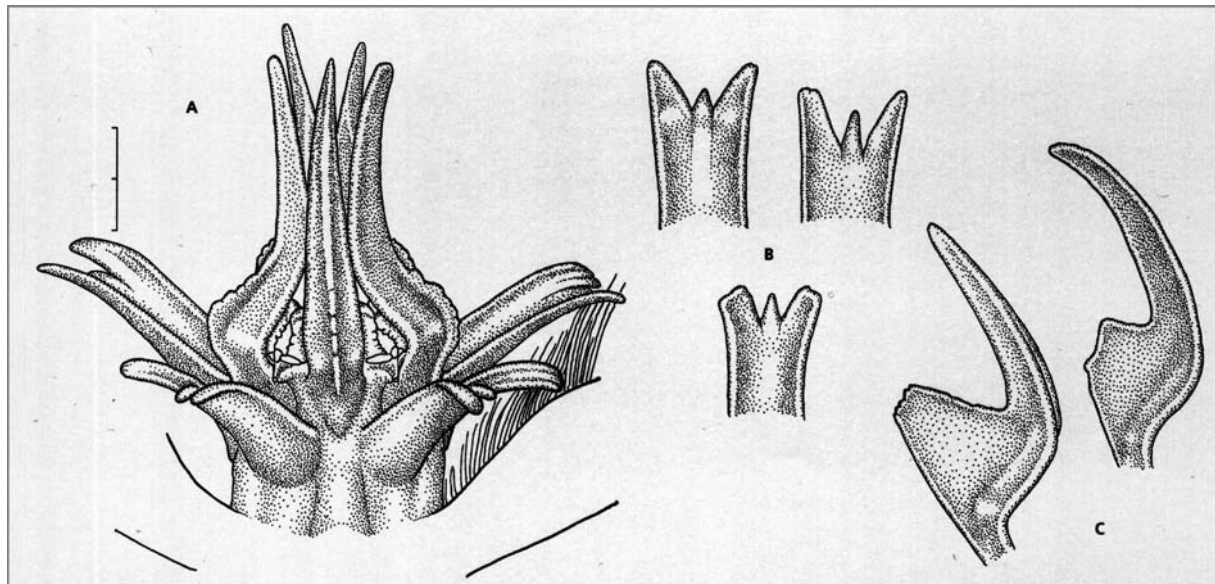


Fig. 15.135. *Stapelia obducta*. A, side view of gynostegium. B, outer corona lobes from above (upper two from same plant as A). C, side view of inner corona lobes (right hand one from same plant as A). Scale bars: all 2 mm (at A). Drawn from PVB 4977, Grootrivier Mountains, north-east of Willowmore.

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from which it is 'easily distinguished by its unique indumentum of fine soft hairs covering the entire inner surface of the corolla, its glabrous pedicel and calyx and inner corona lobes which, although variable, are quite different from any seen in the *S. tsomoensis* material examined' (Leach 1985). This does not correspond with his description (1985: 46), where he gave the pedicel as 'finely, shortly pubescent' in *S. obducta* and that is certainly how they are in my own collections from near Cockscomb so that this difference must be discarded. He added that the inner corona lobes are 'quite different' from those of *S. tsomoensis* but a comparison of his fig. 28 and fig. 31 reveal little of substance except slightly longer, more

spreading lobes and a longer dorsal projection in *S. tsomoensis*. As he admits, those of *S. obducta* are variable. Even in material from Cockscomb, the dorsal projection can be much shorter than he showed it and in some plants it was almost absent. So the significant differences are that *S. obducta* has fine hairs all over the corolla whereas they are restricted to certain patches in its relatives and in *S. obducta* the corolla always has the lobes folded back behind it. The hairiness of the corolla is subject to some variation in that plants from Cockscomb may be nearly glabrous just beyond the middle of the lobes, whereas those from Long Kloof also have a nearly bald patch there. The hairs are usually considerably longer towards the margins of the



Fig. 15.137. *S. obducta*, PVB 4977, Grootrivier Mountains, north-east of Willowmore.



Fig. 15.138. *S. obducta*, PVB 7135, north of Joubertina, Long Kloof. Here the flower is in the process of opening and the lobes are still spread out.



Fig. 15.136. *S. obducta*, PVB 7038, near Cockscomb Peak, south of Steytlerville.

lobes than in their middle.

The pedicel in *S. obducta* is particularly variable and this gives some indication of the variability of most of the characters in this complex. In the specimen seen by Leach, the pedicel held the flower close to the stems and was about 30 mm long and 2 mm thick. In my own material from near Cockscomb Peak (PVB 7038) the pedicel varied from 15 to 50 mm long whereas in my collections from the Long Kloof (PVB 7135) they are 55-60 mm long and 3.5-4.0 mm thick.

The follicles in *S. obducta* are brightly longitudinally striped with purple-red and, in this respect, are unlike those of either *S. hirsuta* var. *baylissii* or var. *tsomoensis*.

History

Stapelia obducta was described from a collection of Lawrence Crawford Mullens (1913-), who found a single large clump on the flats near the northern foot of the Cockscomb Peak (L.C. Mullins, pers. comm. 2000).



Fig. 15.139. *S. obducta*, PVB 8949, Grootrivier Mountains, north-east of Willowmore, showing the typically almost shiny stems and the turban-shaped flower.

STAPELIA GRANDIFLORA

19. *Stapelia grandiflora*

Stapelia grandiflora Masson, *Stap. Nov.*: 13, t.11 (1797).

Gonostemon grandiflorus (Masson) P.V.Heath, *Calyx* 1:17 (1992).

Type: South Africa, Cape, Sundays River, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t.11.

Often large succulent forming compact clump up to 1 m diam. or more. **Stems** 60-300 mm long, 20-40 mm thick, decumbent, shortly pubescent, usually grey-green; **tubercles** widely spaced along stems, not prominent, joined into 4 obtuse angles along stem; **leaf-rudiments** 3-5 mm long. **Inflorescences** pubescent, 1 per stem near base, of 1-5 successively developing flowers on short stout peduncle; **pedicel** 10-70 mm long, 3-5 mm thick, spreading with flower facing $\pm$ horizontally; **sepals** 4-15 mm long, 2-3 mm broad at base, lanceolate, acute. **Corolla** (50-) 80-220 mm diam., rotate usually with strongly recurved lobes; outside pale green with 3-5 raised longitudinal veins; inside transversely narrowly rugulose, ridges purplish red and between them yellow, changing to $\pm$ uniformly purplish red towards apices of lobes and near margin, covered particularly towards (often somewhat papillate) margin with soft mostly white hairs up to 10 mm long; **tube** 5-8 mm long, 15 mm broad, pentagonal, funnel-shaped, caused mainly by thickening in corolla; **lobes** 30-80 mm long, 20-40 mm broad at base, oblong to elliptic or ovate, acute, usually slightly convex from recurved margins. **Corona** 10-12 mm tall, 15-20 mm broad, raised on stout obtusely pentagonal yellow stipe $\pm$ 1.5 mm long, red to purple becoming yellow towards apices and base; **outer lobes** 7-9 mm long, spreading and slightly ascending, linear sometimes broadening towards dentate to acute apex, channelled down upper surface; **inner lobes** 6-11 mm long, incumbent on backs of anthers then erect and slightly recurved near apices, dorsiventrally flattened near base becoming laterally flattened above, acute, with laterally flattened wing-like erect and broad dorsal horn attached in lower half (for most of its length).

Leach (1985) took a broad view of *S. grandiflora* and included under it a host of other names. The main question surrounding this species is whether it is distinct from *S. hirsuta*. There is little in the way of substantial differences between them: only the larger flowers (the areas where *S. hirsuta* has particularly broad flowers lie in the west from Montagu to Malmesbury, nowhere near where *S. grandiflora* occurs) and the very much stouter stems of *S. grandiflora* (often tapering significantly towards their apices) can usually be used to distinguish them. However, they quite often occur together, as for example, around Calitzdorp and Oudtshoorn, Willowmore and Steytleville and as far east as Stutterheim. There appears to be no disintegration of the barriers between them in these areas and so they are maintained here as distinct species.

19a. *Stapelia grandiflora* var. *grandiflora*

Stapelia ambigua Masson, *Stap. Nov.*: 13, t.12 (1797).

Gonostemon grandiflorus var. *ambiguus* (Masson) P.V.Heath, *Calyx* 3: 9 (1993).

Type: South Africa, Cape, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t.12.

Stapelia spectabilis Haw., *Syn. PL Succ.*: 16 (1812).

Lectotype: Bot. Mag. 16: t. 585 (1802).

Stapelia ambigua var. *fulva* Sweet, *Hort. Brit.*, ed. 2: 357 (1830).

Gonostemon grandiflorus var. *fulvus* (Sweet)

P.V.Heath, *Calyx* 3: 7 (1993).

Lectotype: Jacq., *Stap.*: t. 54.

Stapelia grandiflora var. *lineata* N.E.Br., *Gard. Chron.* N.S. 7: 558 (1877).

Gonostemon grandiflorus var. *lineatus* (N.E.Br.)

P.V.Heath, *Calyx* 3: 7 (1993).

Type: Cape, without locality, Barkly 21 (K).

Stapelia obscura N.E.Br., *Gard. Chron.* N.S. 7: 558 (1877).

Lectotype: Jan. 1867, MacOwan 1197 (K).

Stapelia desmetiana N.E.Br., *Gard. Chron.* Ser. 3, 6: 684 (1889).

Gonostemon grandiflorus var. *desmetianus* (N.E.Br.)

P.V.Heath, *Calyx* 3: 7 (1993).

Lectotype: Cape, Little Fish R., MacOwan 2249

(K, holo.; BOL, PRE, SAM, iso.).

Stapelia desmetiana var. *apicalis* N.E.Br., *Gard. Chron.* Ser. 3, 6: 684 (1889).

Gonostemon grandiflorus var. *apicalis* (N.E.Br.)

P.V.Heath, *Calyx* 3: 7 (1993).

Lectotype: Cape, Great Fish River, Juby sub MacOwan (K).

Stapelia flavivestris N.E.Br., *Gard. Chron.* Ser. 3, 44:187 (1908).

Type: Cape, Barkly 21 (K).

Stapelia desmetiana var. *pallida* N.E.Br., *Fl. Cap.* 4 (1): 942 (1909).

Gonostemon grandiflorus var. *pallidus* (N.E.Br.)

P.V.Heath, *Calyx* 3: 7 (1993).

Type: Cape, between Willowmore and Klipplaat, N.S. Pillans 155 (BOL).

Stapelia senilis N.E.Br., *Fl. Cap.* 4 (1): 940 (1909).

Gonostemon grandiflorus var. *senilis* (N.E.Br.)

P.V.Heath, *Calyx* 3: 7 (1993).

Lectotype: Cape, Albany distr., N.S. Pillans 198 (BOL, GRA).

Stapelia desmetiana var. *fergusonae* R.A.Dyer, *Rec.*

Albany Mus. 4:116 (1931).

Gonostemon grandiflorus var. *fergusonae* (R.A.Dyer)

P.V.Heath, *Calyx* 3: 7 (1993).

Type: Cape, Colesberg, Ferguson (GRA).

Corolla inside with hairs over most of surface.

Distribution and habitat

Var. *grandiflora* is probably the best recorded of all southern African stapeliads apart, perhaps, from *Hoodia gordonii*. It is widely if rather scantily distributed over the Great Karoo

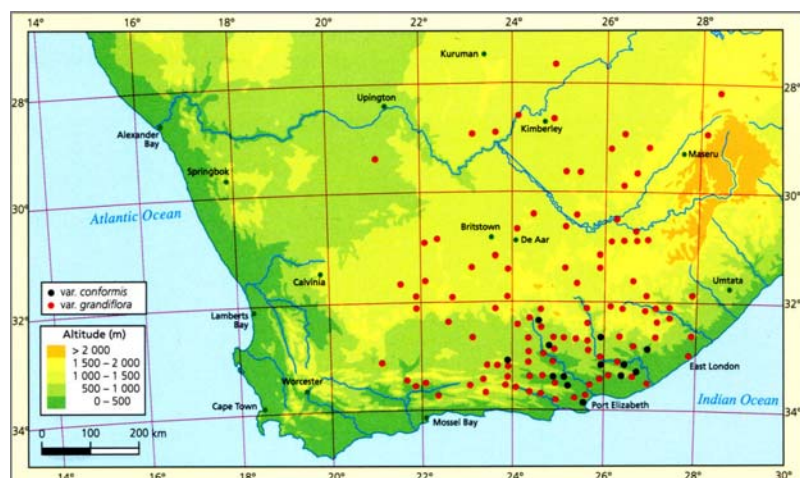


Fig. 15.140. Distribution of *Stapelia grandiflora*.

Key to the varieties of *S. grandiflora*

- Corolla inside with hairs over most of surface, bud usually ellipsoidal 19a. var. *grandiflora*
- Corolla inside with hairs mainly along margins of lobes, bud usually distinctly beaked 19b. var. *conformis*

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from Kenhardt and Carnarvon southwards to around Fraserburg and then east to Graaff-Reinet and into the Free State. There are some records from the Little Karoo from Calitzdorp eastwards to around Willowmore and it is not uncommon in the Steytlerville, Port Elizabeth and Grahamstown areas.

In general, plants are found on the lower, stony slopes of mountains or hills or in flats under trees and they are usually rather widely scattered.

Diagnostic features and relationships

Specimens of var. *grandiflora* can reach an impressive size and may form clumps up to 1 m in diameter or more. As a consequence they are quite conspicuous and it is very likely that this is why they have been so widely recorded. Var. *grandiflora* usually has stout, erect stems which are at least 25 mm in thickness and taper both to the apex and to the base. The tubercles are joined into four robust wings along the stems. The stems are always densely pubescent and this lends them a somewhat greyish hue. Plants can become quite old. In the more geriatric specimens many of the older stems become somewhat rounded and may become



Fig. 15.141. *S. grandiflora* var. *grandiflora*, PVB 7072, north-west of Willowmore.



Fig. 15.142. *S. grandiflora* var. *grandiflora*, PVB 6628, west of Fauresmith, with some eggs from flies on the corolla.



Fig. 15.143. *S. grandiflora* var. *grandiflora*, Inverbolo, north of Stutterheim, in habitat, January 1992.

covered with a corky bark.

The flowers are usually also of an impressive size, mostly 100-150 mm in diameter, but they may exceed 200 mm across on occasion. They generally have broad and long lobes with a fairly small united area in the centre and a very short, pentagonal tube around the base of the gynostegium. Most of the inner surface is covered with fine, transverse ridges which become more or less concentric rings in the central area. Towards the tips, the lobes often have a dark reddish patch but below this the summits of the ridges are yellow while the valleys between them are reddish, creating a finely yellow-lined effect. Fine, white hairs are very variably present on the inside of the flower, sometimes only as cilia up to 10 mm long along the margins, but often they are present all over the interior. In some cases these hairs are so dense as to give the corolla a whitish, bearded appearance. At one time such plants were known as *S. senilis*.

The corona is also quite large and has the same shape as in *S. hirsuta*. The inner lobes are often yellow and this phenomenon gave rise to the name *S. flavirostris*.

History

Var. *grandiflora* was discovered by Francis Masson along the lower reaches of the Sundays River and the plants he collected flowered and were painted in Cape Town in 1792. Leach (1985) was the first to take such a broad view of this taxon, though N.E. Brown (1877) considered at one stage that his *S. flavirostris* was merely a colour variant of *S. grandiflora*.



Fig. 15.144. *S. grandiflora* var. *grandiflora*, PVB 6884, north of Fort Beaufort, showing the typical large and rounded bud.

19b. *Stapelia grandiflora* var. *conformis*

Stapelia grandiflora var. *conformis* (N.E.Br.)

Bruyns, *comb. nov.*

Stapelia conformis N.E.Br., Fl. Cap. 4 (1): 959 (1909).

Stapelia macowanii var. *conformis* (N.E.Br.)

L.C.Leach, *Excelsa Taxon. Ser.* 3: 66 (1985).

Gonostemon macowanii var. *conformis* (N.E.Br.)

P.V.Heath, *Calyx* 1:18 (1992).

Lectotype: Cape, near Grahamstown, cult. Kew, 16 Sept. 1898 (K).

Stapelia macowanii N.E.Br., *Hooker's Icon. PL* 20: t. 1920 (1890).

Gonostemon macowanii (N.E.Br.) P.V.Heath, *Calyx* 1:18 (1992).

Lectotype: Cape, near Grahamstown, Hell's Poort, MacOwan 909 (K).

Stapelia conformis var. *abrasa* N.E.Br., *Fl. Cap.* 4(1):960 (1909).

Gonostemon macowanii var. *abrasus* (N.E.Br.)

P.V.Heath, *Calyx* 3: 8 (1993).

Type: near Great Fish River, Patryshoogte, MacOwan 2247 (K, holo.; SAM, iso.).

Corolla inside with hairs mainly along margins of lobes, otherwise $\pm$ glabrous.

Distribution and habitat

Var. *conformis* has been recorded widely over the Eastern Cape from Graaff-Reinet to Grahamstown and southwards to Willowmore and near Port Elizabeth.

Diagnostic features and relationships

The plant in var. *conformis* is indistinguishable from that of var. *grandiflora*. The buds of var. *conformis* have a much narrower tip and widen from this to near the base, giving them a more top-like or beaked shape. This is somewhat different to those of var. *grandiflora*, where they frequently (but not always) have an ellipsoidal shape with a very rounded and broad apex. The flower in var. *conformis* may reach 155 mm across, though it is commonly 90-120 mm in diameter. Inside, the corolla has the same surface texture and coloration as in var. *grandiflora*, though the colours are often more distinct because of the relative lack of hairs. The surface of the corolla is sparsely pubescent or only minutely pubescent inside the tube and otherwise glabrous. Along the edges of the lobes there are often, though not always, striking white hairs up to 8 mm long which are rather few in number.

Plants of var. *conformis* seem to be of sporadic occurrence over much the same area where var. *grandiflora* is found. There is, in fact, no evidence to suggest that this is anything more than an almost glabrous-flowered variant of *S. grandiflora*. As very similar varia-

tion from densely hairy to practically glabrous flowers is found in *S. hirsuta* (and even in var. *hirsuta*), *S. macowanii* with its var. *conformis* is accorded varietal status under *S. grandiflora* in this treatment.

Stapelia macowanii seems to have been described from an aberrant specimen with small flowers (50-60 mm in diameter) and an unusual inner corona where the dorsal horn was completely fused to the lobe itself (Leach 1985: 65). This material came from Hellspoor, north of Grahamstown. However, several subsequent collections from that area have proved to be typical of *S. conformis* (Leach 1985: 68). The name '*conformis*' is used here for the variety of *S. grandiflora* so as to emphasise the more typical nature of this form rather than the form on which '*macowanii*' was based.

History

Var. *conformis* was discovered by Peter MacOwan, who was the principal of Shaw College in Grahamstown and later taught science at Gill College, Somerset East. He made extensive collections in this area and discovered '*Stapelia macowanii*' at Hell's Poort north of Grahamstown, apparently recording it for the first time in June 1876. Leach (1985) treated *S. macowanii* and *S. conformis* as a species distinct from *S. grandiflora* and recognised two varieties, *S. macowanii* var. *macowanii* and *S. macowanii* var. *conformis*. These are both treated here as a single variety of *S. grandiflora*.

20. *Stapelia gettliffei*

Stapelia gettliffei Pott, *Ann. Transvaal Mus.* 3: 226, t.13(1913).

Gonostemon gettliffei (Pott) P.V.Heath, *Calyx* 1:17 (1992).

Type: South Africa, Transvaal, Louis Trichardt, G.F. Gettliffe sub Transvaal Mus.9643 (PRE).

Succulent forming spreading mat-like clump up to 2 m diam., with many stems. **Stems** 50-150 mm long, 10-15 mm thick, decumbent-ascending and usually somewhat limp and trailing, pubescent, greyish green to green or suffused with red; **tubercles** 2-3 mm long, very obscure and joined for most of length into 4 $\pm$ acute wings along stem between which stem concave; **leaf-rudiments** 6-11 mm long, lanceolate, $\pm$ adpressed to stem. **Inflorescence** pubescent, 1 per stem usually near base, with 1-3 flowers developing in gradual succession on short peduncle < 5 mm long; **pedicel** 50-80 mm long, 3-4 mm thick, spreading on ground with upturned apex to hold flower facing upwards; **sepals** 9-15 mm long, 2 mm broad at base, lanceolate, acute. **Corolla** 90-120 mm diam., rotate, deeply lobed; outside pale green with 5-7 darker veins on each lobe; inside transversely lightly rugulose over whole surface except in tube, with ridges becoming closer together and forming $\pm$ concentric rings on united area, cream on ridges with purple-red between them and along edges of lobes, with fine purplish hairs (up to 10 mm long) towards margins of lobes and in dense cushion in united area becoming shorter towards base of tube; **tube** < 2 mm deep, very shallowly plate-like, cream inside, with corolla somewhat thickened at 'mouth'; **lobes** 40-60 mm long, 20-25 mm broad at base, spreading, narrowly ovate, acute, usually somewhat convex from recurved margins. **Corona** $\pm$ 12



Fig. 15.145. *S. grandiflora* var. *conformis*, PVB 5402, east of Springbokvlakte. The much more beaked bud can be seen on the left.

mm tall, $\pm$ 15 mm broad, dark purple-brown becoming 'eddyish' towards base, raised on short pentagonal stipe < 1 mm long, glabrous; **outer lobes** $\pm$ 5 mm long, ascending then spreading, deeply channelled around middle becoming terete towards apex, apiculate; **inner lobes** 10-12 mm long, 1.0-1.5 mm broad, adpressed to backs of anthers after which erect and connivent in centre then diverging widely, dorsiventrally flattened below becoming ventrally channelled and up to 1.5 mm broad above anthers, with broad $\pm$ deltoid dorsal wing 6-8 mm long, adnate to lobe for most of its length.

Distribution and habitat

Stapelia gettliffei is widespread along the catchment of the Limpopo River. This encompasses parts of south-eastern Botswana, the northern-most parts of South Africa, southern Zimbabwe and a small area in Mocambique near Pafuri. It is also found along the valley of the Sabi River in eastern Zimbabwe.

Plants mainly grow in flat, relatively low-lying areas, often in the shade of trees in stony ground or hard loam. They frequently occur in overgrazed spots with a wide selection of other stapeliads, particularly *Duvalia polita*, *Huernia zebrina*, *Orbea rogersii*, *Stapelia gigantea*, *S. kwebensis* and *Tavaresia barklyi*. Several hybrids have been reported which may involve *S. gettliffei* as one parent.

Diagnostic features and relationships

Stapelia gettliffei has particularly characteristic stems which, when heavily shaded, tend to sprawl on the ground with their upper half ascending. When growing in the open they are more erect and more tightly clustered. In either situation, plants can become large and specimens up to 2 m in diameter are not exceptional. The stems are relatively slender

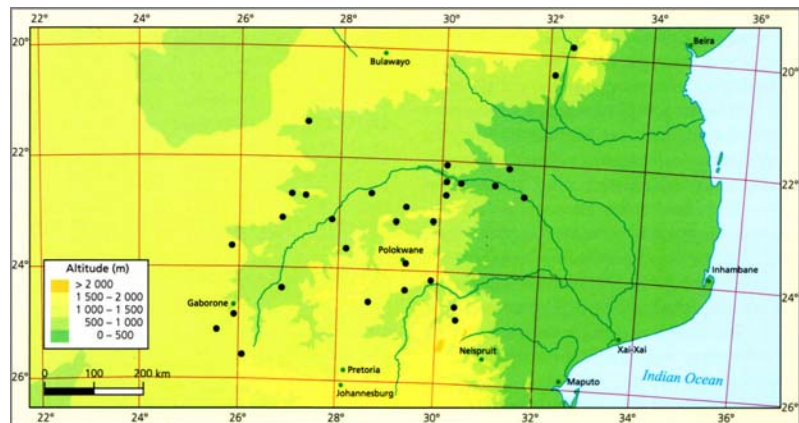


Fig. 15.146. Distribution of *Stapelia gettliffei*.

(usually about 12 mm thick), with the tubercles forming inconspicuous, but not rounded angles along the stem. Each tubercle is tipped by a narrow but long leaf-rudiment - in fact, these leaf-rudiments are the longest in the genus and may reach 10 mm or more. The leaf-rudiments ascend against the stem and persist as dried white husks for some time.

Stapelia gettliffei is another of the comparatively large-flowered species and here the flowers are usually about 100 mm across. They generally lie flat on the ground facing upwards and often there are many of these flowers around the outside of a large plant. The corolla consists of quite long, roughly elliptical lobes, which are gently folded downwards towards the margins and there is a very small united disc in the centre around the corona. Most of the surface of the lobes is covered with low, transverse, cream-coloured ridges interspersed with purple-red, but generally,

the edges of the lobes are lined with plain purple-red. Towards the centre the ridges become closer together and they fade away altogether in the tube. The lobes are glabrous except towards the edges where there are long, fine, purplish hairs, each of which arises from a very small papilla. On the united part below the bases of the lobes there is a dense cushion of fine, often rather matted hairs which become progressively shorter towards the centre. The central disc of the flower is only very slightly sunken around the corona to form a shallow 'tube', but the fabric of the corolla is somewhat thickened around the edge of this sunken area to indicate the 'mouth' of the tube.

The corona of *S. gettliffei* consists of slender outer lobes and relatively massive inner lobes which rise in the centre and spread from there. The inner surface of the inner lobes is distinctly channelled, which is unusual, and the lobes have a prominent, dorsal fin-like horn, as do

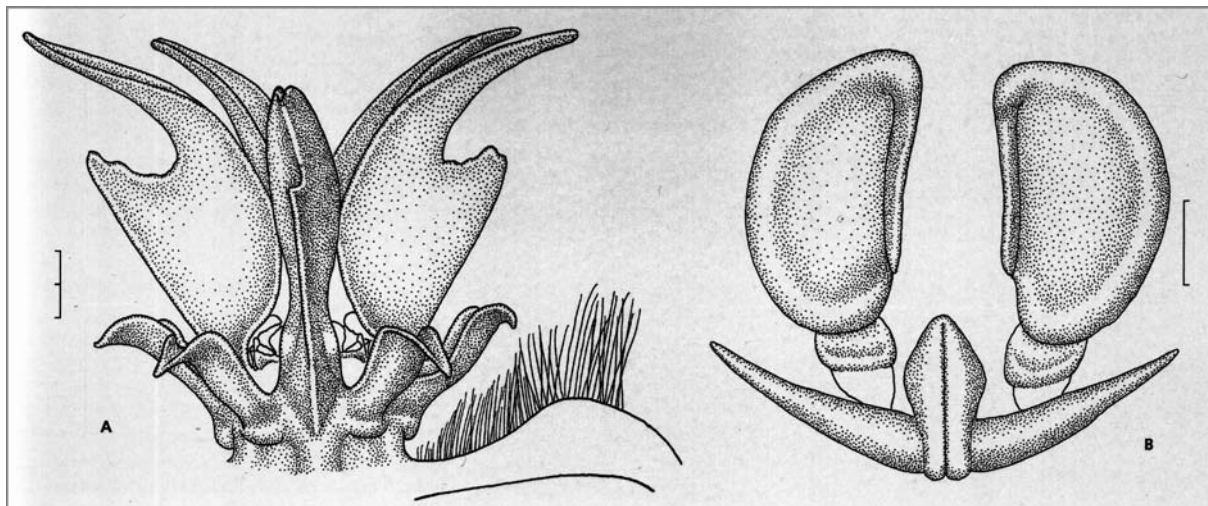


Fig. 15.147. *Stapelia gettliffei*. A, side view of gynostegium. B, pollinarium. Scale bars: A, 2 mm; B, 0.25 mm. Drawn from PVB 6988, Gootau, Botswana.

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several of the large-flowered species.

White & Sloane (1937) and Leach (1985) considered this species to be most closely related to *S. hirsuta* but it is also very similar to *S. grandiflora*. From both of these species *S. gettliffei* is immediately distinguished by the length of the leaf-rudiments as well as by the usually limp and trailing nature of the stems. However, in the flowers there are no clear differences on which to separate *S. gettliffei* from the other two, especially from some of the large-flowered forms of *S. hirsuta*. *Stapelia gettliffei* is also closely allied to *S. gigantea*. These two species are again most easily separated by the differences in the stems and especially since the leaf-rudiments in *S. gigantea* are never more than 3 mm long. The flowers of *S. gigantea* have differently shaped corolla lobes which taper to

a slender tip, whereas in *S. gettliffei* the lobes are acute. The two species are found growing together on occasion.

History

Stapelia gettliffei was discovered by George Frederick R. Gettliffe in March 1911 near Louis Trichardt at the southern base of the Soutpansberg. It was also collected the following month by C. Frank near Palapye in Botswana. The specific name has traditionally been spelled 'gettleffii', which is how its author and how White & Sloane also spelled it. Nevertheless, as H. Hall (1959) first pointed out (repeated by Leach (1980b)), it should have been 'gettliffei'.



Fig. 15.148. *S. gettliffei*, Ga-Mankodi, south of Blouberg near Dendron, in habitat, January 1996.



Fig. 15.149. *S. gettliffei*, PVB 6988, Gootau, Botswana, in habitat, December 1996.

21. *Stapelia gigantea*

Stapelia gigantea N.E.Br., *Gard. Chron.* N.S. 7: 684 (1877).

Gonostemon giganteus (N.E.Br.) P.V.Heath, *Calyx* 1:17(1992).

Lectotype: South Africa, Natal, Gerrard 717 (K).

Stapelia nobilis N.E.Br. ex Hook. f., *Bot. Mag.* 127: t. 7771 (1901).

Gonostemon giganteus var. *nobilis* (N.E.Br.) P.V.Heath, *Calyx* 3: 7 (1993).

Type: cultivated plant, Griffiths (K).

Stapelia marlothii N.E.Br., *Bull. Misc. Inform.* 1908: 436 (1908).

Gonostemon giganteus var. *marlothii* (N.E.Br.) P.V.Heath, *Calyx* 3: 7 (1993).

Type: Zimbabwe, Matopos, Marloth 3414 (K, holo.; PRE, NBG, iso.).

Stapelia gigantea var. *pallida* E.Phillips, *Fl. PL South Africa* 5:t.181 (1925).

Gonostemon giganteus var. *X pallidus* (E.Phillips) P.V.Heath, *Calyx* 3: 7 (1993).

Type: cultivated plant, PRE (missing).

Stapelia youngii N.E.Br., *Bull. Misc. Inform.* 1931: 43 (1931).

Gonostemon giganteus var. *youngii* (N.E.Br.) P.V.Heath, *Calyx* 3: 7 (1993).

Type: Zimbabwe, near Harare, Young sub Herb. Moss. 17301 (K).

Stapelia cylista C.A.Luckh., *S. African Gard. & Country Life* 23:139 (1933).

Type: Vanrhynsdorp distr., hort. Hurling & Neil (missing).

Lectotype (designated here): A.C. White & B.

Sloane, *Stap.*, ed. 2, 2: t. XV, opp. p. 524 (1937).

Succulent forming spreading to dense clump to 1 m diam. or more. **Stems** 100-300 mm long, 12-35 mm thick, erect, shortly pubescent, green suffused or mottled with purple; **tubercles** 1-3 mm long, obscure, joined into 4 prominent wings along stem with broadly concave area between them; **leaf-rudiments** 2-3 mm long, deltoid, acute. **Inflorescences** pubescent, 1 per stem arising near base, with 1-4 flowers developing in gradual succession on short stout peduncle up to 10 mm long with few deltoid bracts $\pm$ 2 mm long; **pedicel** 20-60 mm long, 4-5 mm thick, pinkish, spreading and holding flower facing outwards; **sepals** 7-16 mm long, 3-5 mm broad at base, ovate, acute. **Corolla** 125-400 mm diam., rotate to reflexed, lobed to about three-quarters of radius with flat to campanulate central united area; outside pink to green, with 3-5 darker veins on each lobe; inside transversely rugulose over whole surface with ridges becoming closer together and forming $\pm$ concentric circles on united area and in tube, pale yellow-brown to reddish, with tips of ridges darker red-brown or purple, covered all over with fine hairs, hairs longest (to 15 mm) and thickest and whitish along margins of lobes becoming shorter and more slender and purplish away from margins; **tube** 15-50 mm deep, conical, pentagonal towards base; **lobes** 80-150 mm long, 40-60 mm broad at base, spreading to reflexed, ovate, acuminate, flat towards base becoming somewhat

convex with reflexed margins in slender portion. **Corona** $\pm 12-19$ mm tall, $\pm 13-15$ mm broad, dark purple, raised on yellow pentagonal stipe 1-2 mm tall, glabrous; **outer lobes** 5-7 mm long, 1.5-2.5 mm broad, ascending then spreading, rectangular to oblong or sub-spathulate, with crenulate or acute to acuminate apex; **inner lobes** 8-12 mm long, 1-2 mm broad, adpressed to backs of anthers then erect and connivent in centre, dorsiventrally flattened below becoming nearly terete above, with broad $\pm$ oblong erect dorsal wing up to 11 mm long.

Distribution and habitat

Stapelia gigantea is the most widely distributed species of *Stapelia* in a north-south direction. Plants have been collected in Zambia and Malawi and over a very wide area in Moçambique. In all these countries the collections are few and extremely widely dispersed. They are also recorded (Leach 1985) from Kenya and Tanzania but both these specimens are most

likely to have been escapes from gardens and it seems that *S. gigantea* is not indigenous there. In Botswana it is found along the eastern side, from Nata southwards to near Lobatse. It is widespread in the lower-lying parts of Zimbabwe and in the north-eastern parts of South Africa. In KwaZulu-Natal, the southernmost records have been made near Stanger,

Over this vast area *S. gigantea* occurs in a wide variety of habitats. These range from stony or loamy flats among trees, to rocky slopes and granite domes (as at Cape Maclear along the shores of Lake Malawi) or even coastal sands among bushes alongside mangrove swamps, as in the coastal areas of central Moçambique. In northern South Africa, Botswana and Zimbabwe it often occurs with *S. gettliffei* and several other stapeliads in overgrazed areas around villages among and under shrubs of *Acacia*.

Diagnostic features and relationships

Stapelia gigantea forms large clumps of robust stems which may exceed 1 m in diameter and reach 3 m across on occasion. The stems are erect and strongly 4-winged but they have very obscure tubercles which hardly project from the surface of these angles.

The flowers of *S. gigantea* are usually at least 200 mm across and may reach a diameter of 400 mm, which is amongst the largest in the



Fig. 15.150. *S. gigantea*, south of Ellisras, in habitat, January 1996.

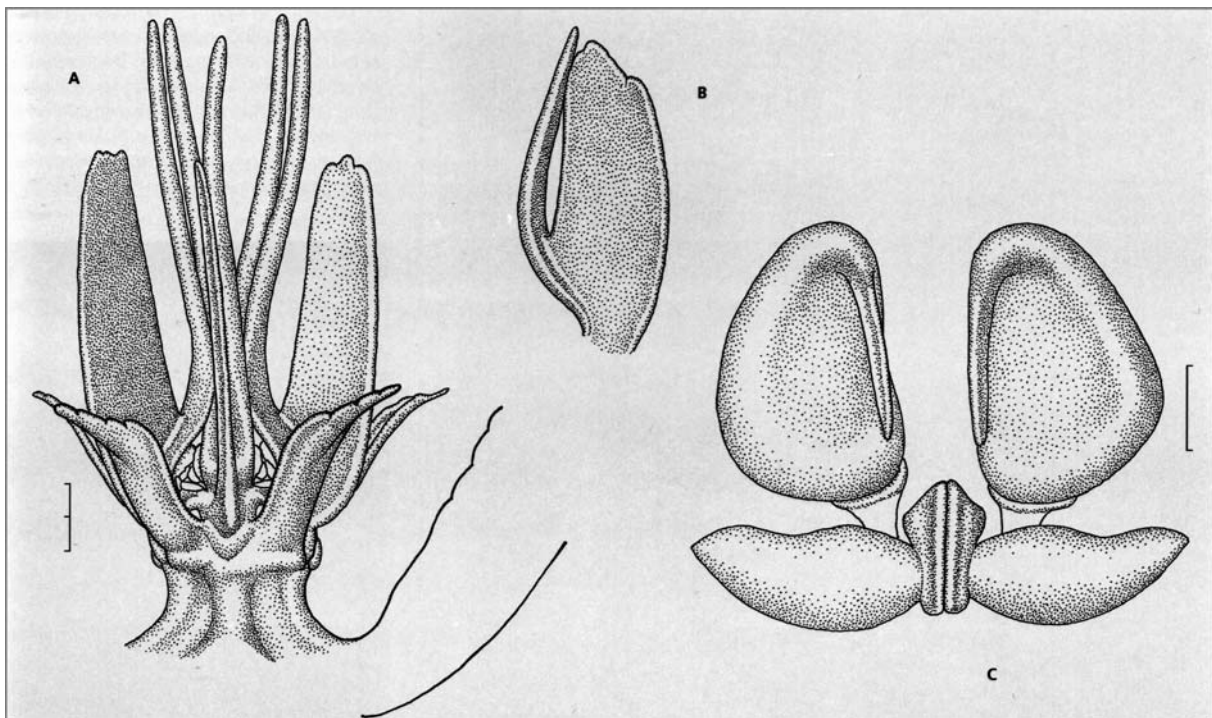


Fig. 15.151. *Stapelia gigantea*. A, side view of gynostegium. B, side view of inner corona lobe. C, pollinarium. Scale bars: A, B, 2 mm (at A); C, 0.25 mm. Drawn from A, C, PVB 6980, Nata River, Botswana; B, PVB 6650, Boka'a Dam, near Gaberones, Botswana.

STAPELIA GIGANTEA

plant kingdom. They tend to be smaller towards the northern limits of the distribution. A general feature of the flower is the long, fairly narrow lobes which attenuate into slender tails and this is visible already in the bud, which has a slender attenuated beak. The centre is particularly variable in shape and may be practically flat (disc-like) with a small depression around the gynostegium or it may be deeply conical. The

corolla becomes gradually thicker below the bases of the lobes to reach nearly 3 mm thick around the corona but it does not possess any kind of definite annular thickening. The inside is always covered with fine purplish hairs which reach their greatest length and palest colour along the margins. All over the surface of the lobes there are transverse, raised reddish ridges. In the tube or on the central disc these

ridges become closer together and much finer and, along with a denser covering of hair, this causes the colour to become darker towards the centre. An unpleasant odour is given off, but it is not as strong as one might expect from so large a flower.

In *S. gigantea* the corona is comparatively large and the whole gynostegium may be up to 18 mm tall. The corona lobes are usually purplish red but the whole structure becomes yellow at the base and on the stipe. The outer lobes are narrow and channelled above, spreading outwards but not pressed to the surface of the tube. The inner lobes are long and slender with a flattened, tall dorsal fin more or less parallel to them.

Stapelia gigantea is easily separated from other large-flowered species such as *S. gettlif-feri*, *S. grandiflora* and *S. hirsuta* (but not from *S. unicornis*) by the manner in which the corolla lobes taper to slender tips. Vegetatively, the narrower angles on the stems may separate it from *S. grandiflora* and they clearly separate it from *S. hirsuta*, where the angles are always far more obscure.

History

N.E. Brown published his account of *S. gigantea* in 1877. He based it partly on two illustrations made in Natal by W. John Sanderson, one of which was printed together with Brown's description, and also partly on a specimen collected by William T. Gerrard between 1861 and 1865 in Natal. Sanderson's drawings were made from material grown in Durban which flowered in 1860. This material was collected by Robert W. Plant on his last expedition of 1858, during which he died at St Lucia. After his death his servants brought the specimens he had collected and his other possessions back to Durban.



Fig. 15.152. *S. gigantea*, PVB 6650, Boka'a Dam, near Gaborone, Botswana.

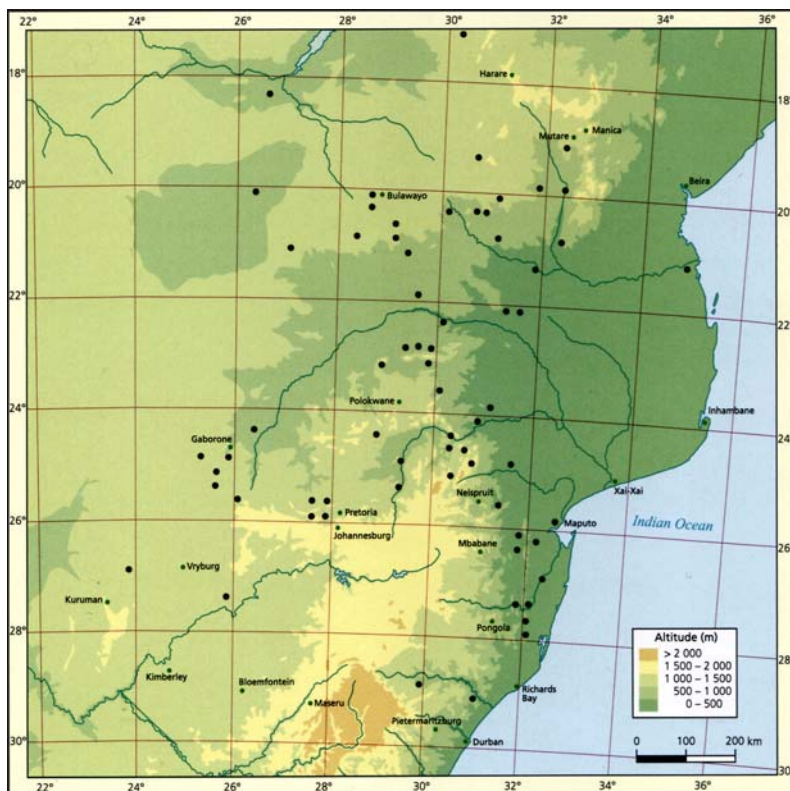


Fig. 15.153. Distribution of *Stapelia gigantea*.



Fig. 15.154. *S. gigantea*, near Nelspruit, in habitat, March 1994 (photo: G.D. Tribe).

22. *Stapelia unicornis*

Stapelia unicornis C.A.Lückh., 'S. A. G.' 28: 228 (1938).

Gonostemon unicornis (C.A.Lückh.) P.V.Heath, *Calyx* 1:17(1992).

Type: Swaziland, Bergplaats, *Postma sub Lückhoff* 258 (BOL).

Succulent forming clumps of loosely packed stems, 150-500 mm diam. **Stems** 60-160 mm long, 10-15 mm thick, decumbent with distinctly horizontal base, pubescent, pale green; **tubercles** 3-5 mm long, fused into 4 thick obtuse angles along stem with concave area between angles; **leaf-rudiments** 2.0-2.5 mm long. **Inflorescence** softly pubescent, 1 per stem, of 1-5 flowers developing in gradual succession from short stout peduncle near base of stem with lanceolate bracts 3-5 mm long; **pedicel** 8-30 mm long, 3 mm thick, spreading and holding flower facing horizontally; **sepals** 5-10 mm long, 2-3 mm broad at base, ovate, acute. **Corolla** 80-130 mm diam., $\pm$ rotate to shallowly campanulate; outside cream to pink with darker veins (3-5 per lobe); inside transversely rugulose with rugulosity red-brown and rest pale yellow often becoming reddish towards tips of lobes, covered with fine purple to red hairs that are longest (10 mm) and thickest in tube and along margins of lobes, densest in tube and more scanty towards tips of lobes, becoming shorter and more slender and purplish away from margins; **tube** $\pm$ 5 mm deep, shallowly bowl-shaped below lobes with slightly thickened portion closer to centre; **lobes** 45-60 mm long, $\pm$ 25 mm broad at base, spreading to reflexed, ovate, acuminate, slightly convex above from recurved margins. **Corona** $\pm$ 10 mm tall, $\pm$ 12 mm broad, with short broad pinkish pentagonal stipe 1.0-1.5 mm tall, dark purple, glabrous; **outer lobes** 5-6 mm long, 1 mm broad, linear, acuminate to acute, concave above, ascending then recurved near apex; **inner lobes** 7-9 mm long, lanceolate, initially adpressed to backs of anthers then connivent-erect, dorsiventrally flattened and becoming terete towards apex, with 3-4 mm wide laterally flattened dorsal wing fused to it for most of length.

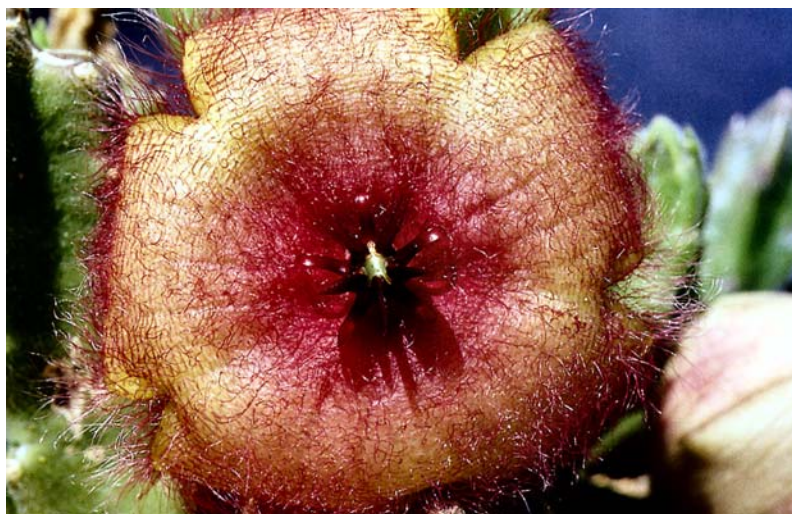


Fig. 15.155. *S. unicornis*, PVB 4457, near Jozini Dam.

Distribution and habitat

Stapelia unicornis is mainly confined to the southern 150 km of the Lebombo Mountains from south of Komatipoort to near the Jozini Dam in KwaZulu-Natal. It is found in Mozambique, South Africa and Swaziland along these mountains more or less where these three countries meet. It also occurs along the Bhivane River (Leach 1985), a tributary of the Pongola River, to some 30 km east of Vryheid in KwaZulu-Natal, and nearly 100 km west of the Lebombo Mountains. It may well prove to be more widely distributed along the Pongola River and its tributaries.

Plants grow on the slopes and summits of mountains or hills in shallow soils on ledges and rocky outcrops. They occur on sandstones and igneous rocks.

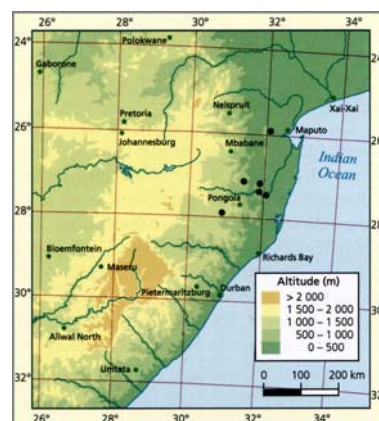


Fig. 15.156. Distribution of *Stapelia unicornis*.

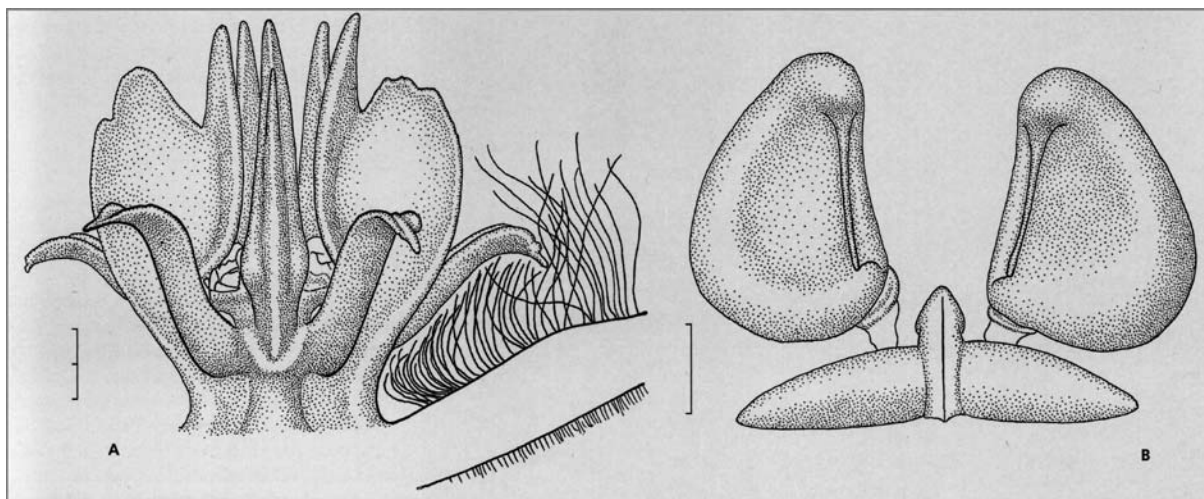


Fig. 15.157. *Stapelia unicornis*. A, side view of gynostegium and part of centre of corolla. B, pollinarium. Scale bars: A, 2 mm; B, 0.25 mm. Drawn from PVB 4457, near Jozini Dam.

STAPELIA LEENDERTZIAE

Diagnostic features and relationships

Specimens of *S. unicornis* often form large, somewhat diffuse clumps. The stems mostly remain comparatively short and, when grown in a sunny spot, they rarely exceed 100 mm long. They have a distinctive pale green colour and are covered with comparatively long hairs. This alone makes *S. unicornis* quite easily recognisable. The tubercles form relatively low wings along the stems but are themselves quite clearly visible.

The flowers in *S. unicornis* are usually around 100 mm in breadth. They have relatively long lobes, which occupy about three-quarters of the diameter of the flower and taper to slender tips similar to those of *S. gigantea*. The central united portion is very variable in shape, from nearly flat to quite deeply bowl-shaped. It has a distinct thickening near the base, just below the tips of the outer corona lobes. Inside, the flower has transverse, raised, reddish lines on a pale yellow background, with the lines becoming closer towards the centre. It is covered with fine, reddish hairs which reach a length of 10 mm in the tube and along the margins of the lobes.

The outer corona lobes are quite slender and slightly channelled inside, with an acute, recurved tip. The inner lobes rise in the centre and each is fused almost to its tip to its comparatively large and broad dorsal horn. This makes it appear as if the inner lobes consist of a single, broad, flattened horn and is the reason for the name that Carl Lückhoff gave to this species. However, the real inner lobe remains clearly visible since its tip may project beyond the broad fused part and the lobe itself is always

much thicker than the dorsal horn.

In many respects *S. gigantea* and *S. unicornis* are very similar. However, as Leach (1980b) made clear, there is every reason to believe that one is dealing here with two distinct species. The two occur close to one another over most of the range of *S. unicornis* but do not appear to either intergrade or hybridise. The distinctive colour of the stems and their comparatively long hairs make *S. unicornis* vegetatively easy to recognise. The flowers of *S. unicornis* are much smaller than those of *S. gigantea* in this area but it is in the corona where the most obvious difference is to be found. In *S. unicornis* the dorsal horn of the inner lobe is fused to the lobe for the whole of its length whereas in *S. gigantea* it is only fused at its base.

History

Stapelia unicornis seems to have been discovered by Donald Robert Keith (see *Orbea carnosa*), during or just before 1935, and he sent plants to the Botanical Research Institute in Pretoria. They flowered in 1935 and it was from these that the first specimens were made.

Miss S. Postma collected this species on the farm Bergplaats in Swaziland and her plants were grown by a Miss W. de Villiers in Cape Town. Miss de Villiers supplied Carl Lückhoff with a flowering plant in May 1937 and it was from this that he described *S. unicornis*. He deposited a specimen from Bergplaats in the Bolus Herbarium and there is no reason not to assume that this is the specimen on which he based the description. It must, therefore, be the holotype and I see no point in treating it as a neotype as Leach (1980b) did.



Fig. 15.158. *S. unicornis*, PVB 4457, near Jozini Dam.

23. *Stapelia leendertziae*

Stapelia leendertziae N.E.Br., *Ann. Transvaal Mus.* 2: 168 (1910).

Gonostemon leendertziae (N.E.Br.) P.V.Heath, *Calyx* 1: 17 (1992).

Type: South Africa, Transvaal, near Heidelberg.

Leendertz 2462 (K, holo.; PRE, SAM, iso.).

Stapelia wilmaniae C.A.Lückh., *S. African Gard. & Country Life* 23:140 (1933).

Type: from Barberton, cult. Lückhoff (missing).

Lectotype (selected here): photo with inset sketches, *S. Afr. Garden. & Country Life* 23:139 (1933).

Succulent forming lax clumps to 0.5 m diam. **Stems** 80-200 mm long, 10-25 mm thick, decumbent with short ascending base, shortly pubescent, green with purple mottling towards tips (if exposed); **tubercles** 1-2 mm long, obscure, joined into 4 obtuse angles along stem with stem distinctly concave between angles; **leaf-rudiments** 2-3 mm long. **Inflorescence** pubescent, 1 per stem arising near base of stems, with 1-3 flowers developing in gradual succession on short stout peduncle up to 10 mm long, with few ovate acute bracts up to 2 mm long; **pedicel** 20-30 mm long, 5 mm thick, spreading and holding flower facing $\pm$ horizontally; **sepals** 6-14 mm long, 3-5 mm broad at base, ovate to lanceolate, acute. **Corolla** 70-100 mm long, 90-120 mm diam., campanulate to urceolate; outside dark purple to reddish purple with darker longitudinal veins; inside finely transversely rugulose over whole surface, dark purple to reddish purple, with slightly clavate purple hairs up to 6 mm long concentrated towards centre and along margins of lobes; **tube** 55-80 mm long, 70-80 mm broad at base, cupular and often narrowing towards mouth; **lobes** 40-50 mm long, 35-45 mm broad at base, spreading, deltate (sometimes broader than long), acuminate, flat towards bases but convex with margins folded downwards, margins with fine hairs. **Corona** $\pm$ 13-15 mm tall, $\pm$ 10 mm broad, glabrous, with pinkish to yellow stipe 2-3 mm tall; **outer lobes** $\pm$ 3 mm long, deeply bifid into attenuate divergent acute lobules, concave above near base, ascending, reddish; **inner lobes** 9-10 mm long, linear, initially adpressed to backs of anthers then slightly spreading, dorsiventrally flattened, with $\pm$ 2 mm wide laterally flattened $\pm$ equally long dorsal wing fused to it near base, dark purple.

Distribution and habitat

Stapelia leendertziae is very well known and widely grown in gardens in southern Africa but it is distinctly uncommon in the field and has not been collected often. It is found in the mountains of the north-eastern escarpment of South Africa from the Abel Erasmus Pass southwards to Barberton and Komatiport, from where records continue into Swaziland. Many collections have also been made around Heidelberg, south of Johannesburg, and it has also been recorded twice from around Ladysmith in KwaZulu-Natal.

Stapelia leendertziae always seems to grow on rocky ground, on slopes or on flat areas with

shallow soils which are derived from sandstones or dolomite.

Diagnostic features and relationships

Plants of *S. leendertziae* form clumps which become large but the stems have a slightly spreading base and this causes the clusters to be fairly lax. The stems are distinctive, being tall but markedly more slender than those of *S. gigantea* or *S. grandiflora*. The distinctly obtuse angles along the stem also do not project as much as in *S. gigantea* and the tubercles are even less prominent than in *S. gigantea*. They are in fact only detectable along the angles by the presence of a minute leaf-rudiment at their upper end.

Stapelia leendertziae is remarkable in the genus for its large and very conspicuously bell-shaped flower. Flowers with deep corolla tubes are common in *Huernia* and other genera such as *Stapeliopsis* but in *Stapelia* (as in *Orbea*) the flowers are typically flat with only a small tube right in the centre. In *S. leendertziae* the corolla consists mostly of the tube, which is usually longer than broad and is also longer than the lobes. Both the inside and the outside of the flower are a uniformly deep reddish purple. The inside of the corolla is very obviously transversely rugulose but it lacks the fine

yellowish striations that are common in most other large-flowered species of *Stapelia*. Hairs are found inside the flower mainly along the margins of the lobes and in a dense beard in the lower quarter of the corolla, so that the corona nestles amongst them. In the flowers that I have seen these hairs are all somewhat clavate, with those along the margins of the lobes more so than those in the tube. The flower emits a weak unpleasant odour and those observed in Cape Town seemed mainly to attract small drosophilid flies rather than the larger types of fly.

In *S. leendertziae* the corolla tube is about 1 mm thick just below the lobes and gradually thickens to about 3 mm around the level of the outer corona so that the lower half of the tube is quite rigid and strong. Below this it abruptly narrows again to less than 2 mm thick and this thinner part forms a small 'primary' tube around the basal stipe of the gynostegium.

The corona in *S. leendertziae* takes up most of the space in the base of the tube and is quite tightly surrounded by firm, curly hairs which entirely fill the space around its lower parts. The stipe, which is much paler than the rest of the corona, fits closely into the basal part of the corolla tube, and the outer corona lobes also spread somewhat to close off the area around the corona. They are unusual for *Stapelia* in that they are deeply divided into fine, diverging lobules. The inner corona is typical of the

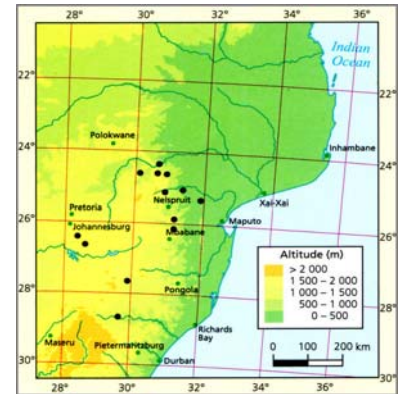


Fig. 15.159. Distribution of *Stapelia leendertziae*.

large-flowered species in having slender lobes with large dorsal projections, each of which is more or less as long as the lobe itself.

While obviously closely allied to such species as *S. gigantea* and *S. gettliffei*, *S. leendertziae* is one of the most distinctive species and, with its deeply campanulate to urceolate, uniformly coloured corolla, can be confused with no other. The shape of the outer corona lobes is also unique in the genus.

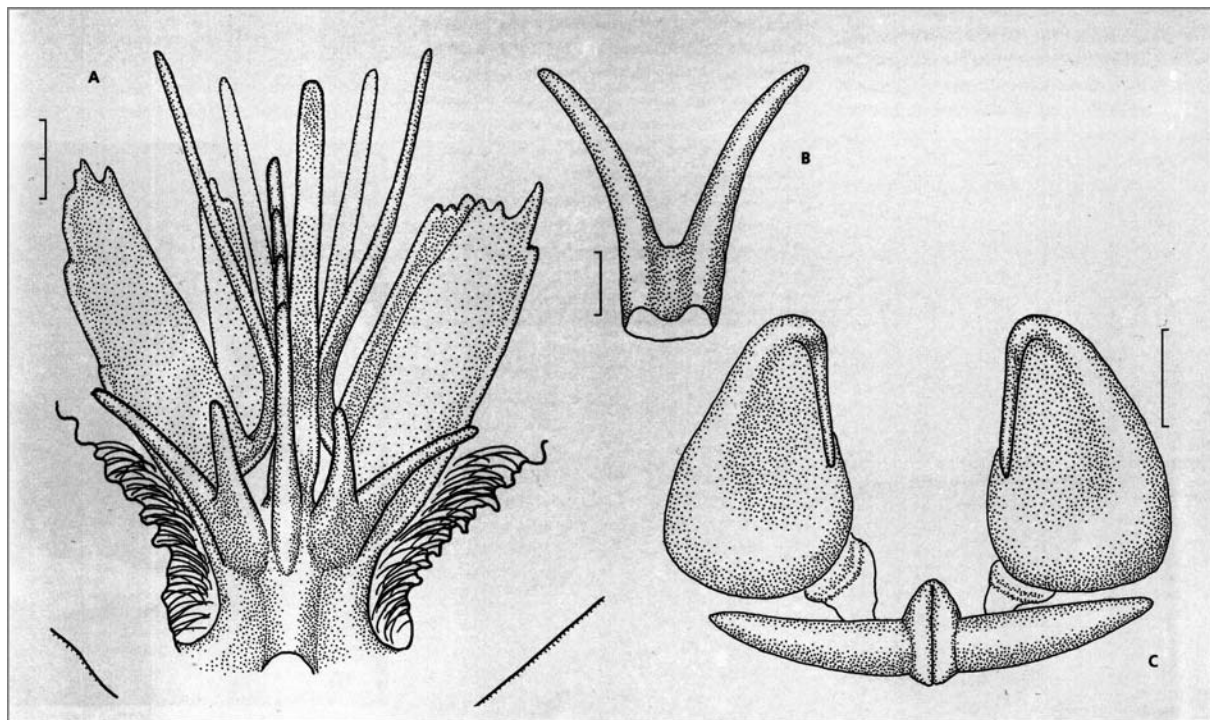


Fig. 15.160. *Stapelia leendertziae*. A, side view of gynostegium and part of centre of corolla. B, face view of outer corona lobe. C, pollinarium. Scale bars: A, 2 mm; B, 1 mm; C, 0.25 mm. Drawn from PVB 7015, Abel Erasmus Pass.

STAPELIA VILLETIAE



Fig. 15.161. *S. leendertziae*, PVB 7015, Abel Erasmus Pass.

History

This species was first collected in November 1909 by Reino Leendertz (later Mrs. Pott), a Dutch lady who was the first official botanist to be appointed in the then Transvaal. She found it near Heidelberg, which is one of the few areas where it has been collected fairly often.

In 1933 Carl Lückhoff described a further species with an even more urceolate corolla. This was *S. wilmaniae*, which he named after Maria Wilman, who sent some plants to him but apparently did not collect them. As discussed by Leach (1985), most of the characters which Lückhoff used to separate his species from *S. leendertziae* can be matched in *S. leendertziae* itself and he reduced *S. wilmaniae* to a synonym of *S. leendertziae*.

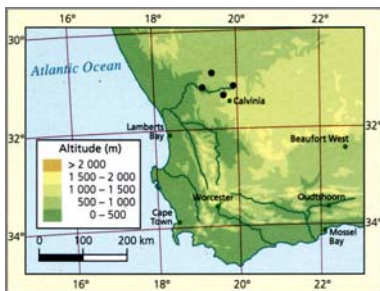


Fig. 15.162. Distribution of *Stapelia villetiae*.

24. *Stapelia villetiae*

Stapelia villetiae C.A.Lückh., 'S.A.G.' 28: 228 (1938).

Gonostemon villetiae (C.A.Lückh.) P.V.Heath, *Calyx* 1:18(1992).

Type: South Africa, Cape, Calvinia Distr., C.T. & E. Villet sub Lückhoff 265 (missing).

Neotype: Calvinia distr., Stayner (NBG).

Succulent forming diffuse to dense clump up to 300 mm diam. **Stems** 60-150 mm long, 10-20 mm thick, decumbent, shortly pubescent, green to purple-green; **tubercles** widely spaced along stem, fairly prominent, joined into 4 obtuse angles along stem with area concave between them; **leaf-rudiments** 1-2 mm long, erect to slightly spreading. **Inflorescences** pubescent, 1 per stem near base, with 1 (-3) flowers with at most short peduncle; **pedicel** 50-65 mm long, 3-4 mm thick, erect and holding flower facing upwards; **sepals** 6-8 mm long, 1.5-2.0 mm broad at base, lanceolate, acute. **Corolla** 45-65 mm diam., rotate; outside pale green to brown with 3-5 darker veins; inside irregularly transversely rugulose on lobes changing to concentric raised ridges towards centre, dark purple-black in upper half of lobes, rest pale yellow with purple-black between ridges, $\pm$ glabrous except for purplish hairs up to 3 mm long along margins of lobes; **tube** $\pm$ 3 mm long, 8-10 mm broad, pentagonal, containing most of gynostegium, walls slightly thickened towards mouth; **lobes** 15-20 mm long, 13-15 mm broad at base, spreading to reflexed, ovate to broadly ovate, shortly acuminate, often convex from folded back margins. **Corona** $\pm$ 5-6 mm tall, $\pm$ 7-8 mm broad, raised on very short pentagonal stipe, black to reddish purple; **outer lobes** 2.0-3.5 mm long, 2 mm broad, ascending then spreading, rectangular to oblong, acute to apiculate or crenulate, channelled down middle; **inner lobes** 2.5-3.0 (-5.0) mm long, adpressed to backs of anthers and exceeding them to rise in short column in centre, dorsiventrally flattened towards base becoming $\pm$ terete towards apex, with spreading triangular to obtuse dorsal wing 0.5-2.0 mm long.

Distribution and habitat

Stapelia villetiae is found in the hilly country between Calvinia, Nieuwoudtville and Loeriesfontein and has most frequently been recorded along the northern aspect of the Hantam Mountains. In this area it grows under bushes on slopes of bluish shales strewn with dolerite rocks.

Specimens have mostly been seen on north-facing, reasonably densely vegetated slopes which are mainly covered with *Pteronia incana*, a species of *Eriocephalus* and *Euphorbia mauritanica*. Plants are generally few and rather scattered in their occurrence.

Diagnostic features and relationships

The stems of *S. villetiae* are more concave between the angles with slightly more obvious tubercles than in the other two species which occur in the same area, namely *S. acuminata* and *S. arenosa*.

In *S. villetiae* the inflorescences bear few flowers (often only one) and the flower is borne facing upwards on a stout and relatively long pedicel. These long pedicels also serve to separate it clearly from any other species growing in the area.

The relatively large flowers are strikingly coloured inside with the upper half of the lobes dark and the rest pale yellow with transverse dark purple lines changing to concentric rings of pale yellow and dark purple near and inside the tube. The whole inner surface is transversely rugulose with low ridges. Along the margins the lobes are adorned with spread-



Fig. 15.163. Elizabeth M. Villet, sitting in the Karoo packing collections of plants, probably sometime in the 1930s (courtesy Cynthia Villet).



Fig. 15.164. *S. villetiae*, PVB 1417, near Toren, north-west of Calvinia.



Fig. 15.165. *S. villetiae*, PVB 1417, near Toren, north-west of Calvinia.

ing purplish hairs but otherwise the flower is more or less glabrous. In most cases the flower is nearly completely flat, with broad, fairly short lobes and a small tube in the centre which contains most of the corona.

The corona in *S. villetiae* consists of short, but broad outer lobes which spread towards the sides of the tube. The inner lobes are also fairly short and rise in a small column in the centre. They have a small dorsal fin. The whole structure is dark and nearly black, sometimes with paler patches towards the tips of the outer lobes.

In most of its floral characteristics *S. villetiae* is more similar to *S. cedrimontana* than to the other species that occur nearby (*S. acuminata* and *S. arenosa*). It differs fairly obviously from *S. cedrimontana* in the erectly held flowers which have broader corolla lobes and in the considerably thicker pedicels. The relatively stout stems with concave sides are also somewhat reminiscent of those in some forms of *S. hirsuta* and several characters (particularly the stout pedicels, stout stems and relatively large flowers) suggest a relationship with other large-flowered taxa.

The experiments of M. Bruce Bayer at the Karoo Garden during the period 1980-7 showed that this is one of the few species of *Stapelia* that is definitely self-fertile (Leach 1985).

History

Stapelia villetiae was discovered by Elizabeth Maria 'Lilla' Villet (nee Brink, 1903-75) between Calvinia and Loeriesfontein sometime before 1938. Mrs. Villet and her husband Charles were enthusiastic collectors of succulents and they discovered several new taxa in the more remote parts of the Western Cape.

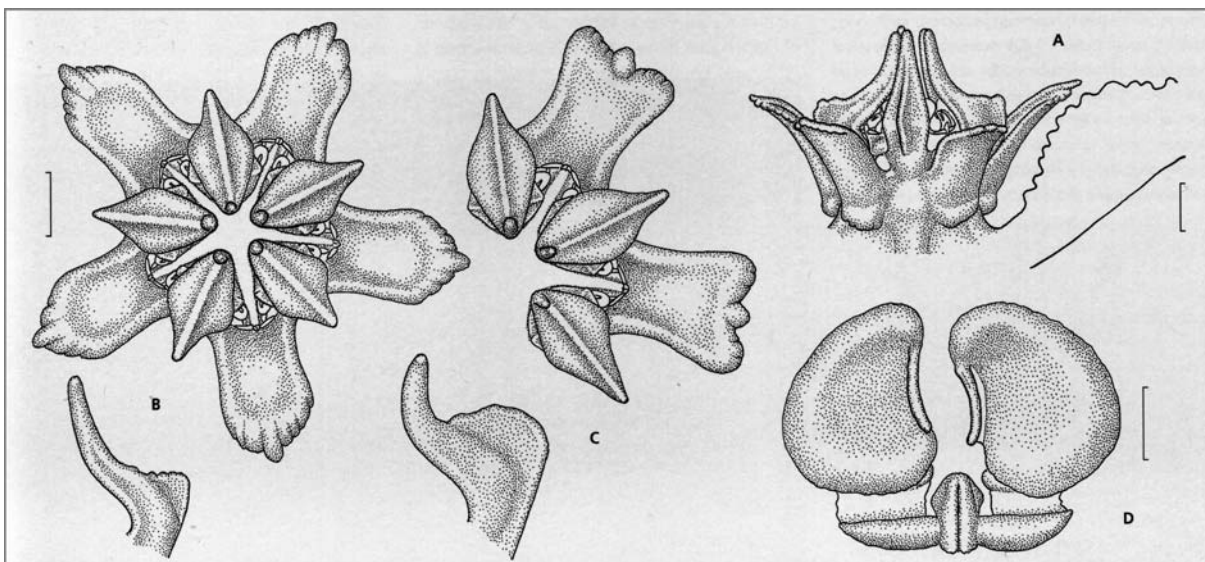


Fig. 15.166. *Stapelia villetiae*. A, side view of gynostegium and part of centre of corolla. B, C, face view of gynostegium (in each case with one inner corona lobe in side view). D, pollinarium. Scale bars: A, 1 mm; B, C, 1 mm (at B); D, 0.25 mm. Drawn from A, B, D, PVB 1417, near Toren, north-west of Calvinia; C, PVB 1353, near Toren, north-west of Calvinia.

STAPELIA CLAVICORONA

25. *Stapelia clavicorona*

Stapelia clavicorona I. Verd., *Fl. PL South Africa*
11: t. 407 (1931).

Gonostemon clavicoronus (I. Verd.) P. V. Heath, *Calyx*
1: 18 (1992).

Type: South Africa, Transvaal, Soutpansberg,
Wyllies Poort, *Van Nouhuys sub PRE 9756* (PRE).

Succulent shrublet forming rather few-stemmed clumps, 150-500 mm diam. **Stems** 50-150 (-200) mm long, 15-50 mm thick, decumbent to erect, stout, shortly pubescent, green mottled with purple; **tubercles** 3-10 mm long, deltoid, joined towards base into 4 wing-like angles along stem between which stem deeply concave; **leaf-rudiments** 1.5-2.0 mm long. **Inflorescence** shortly pubescent, 1-3 per stem mainly towards bases of stems, each with 1-3 flowers developing in gradual succession on short stout peduncle < 5 mm long with a few lanceolate bracts 1-2 mm long; **pedicel** 4-6 mm long, 2.5-3.5 mm thick, spreading and holding flower facing $\pm$ horizontally; **sepals** 3-5 mm long, 2.0-2.5 mm broad at base, ovate-deltoid, acute. **Corolla** 45-60 mm diam., rotate; outside shortly pubescent (becoming longer towards tips of lobes), green to purplish with 5-7 or more darker veins running down each lobe, often speckled in ring above sepals; inside irregularly transversely rugulose (on united part forming concentric circles), yellow- to green- to purple-brown (rugulosities slightly darker), glabrous except in tube; **tube** 2 mm deep, pentagonal, quite closely surrounding stipe of gynostegium, corolla somewhat thickened around mouth, lower half with many cylindrical downward-pointing purplish hairs; **lobes** 15-18 mm long, 14-19 mm broad at base, broadly ovate, shortly acuminate, $\pm$ flat above becoming convex towards tips where margins reflexed, margins with white to purple vibratile slightly clavate cilia up to 3 mm long except towards apices. **Corona** $\pm$ 5 mm tall, $\pm$ 7 mm broad, raised on stout white obtusely pentagonal stipe $\pm$ 1 mm tall, with somewhat glistening surface, purple-black becoming reddish towards base, glabrous; **outer lobes** 2.0-2.5 mm long, ascending and spreading at mouth of tube, acute, deeply channelled on upper surface; **inner lobes** $\pm$ 3 mm long, adpressed to backs of anthers then erect and connivent, dorsiventrally flattened below, cylindrical-clavate above, with slightly laterally compressed ascending dorsal horn a little larger than lobe itself and also clavate.

Distribution and habitat

Stapelia clavicorona is of fairly restricted distribution and is apparently confined to the sandstones of the Soutpansberg of Limpopo Province. According to Leach (1985: 76) it is 'restricted to a small area in the Soutpansberg in the vicinity of Wyllie's Poort' and all the specimens that he cited came from this spot. My own exploration has revealed that it is considerably more widely distributed. Material has been located from near the north-western corner of the Soutpansberg near Soutpan via Waterpoort to Wyllie's Poort and eastwards at least to Nwanedi. This amounts to a total distance of at least 100 km in an east-west direction along the mountain chain.

Plants grow on hot, stony slopes, usually on the northern aspect and generally not near the base of the mountains but some distance up, at altitudes of 1 000-1 300 m. Larger plants are mostly found in the open or between rocks and they only sometimes shelter beneath a bush. In Wyllie's Poort and eastwards they are often associated with 'forests' of *Androstachys johnsonii*, the Lebombo ironwood, which clothe most of the dry, north-facing slopes to the east of Waterpoort.

Diagnostic features and relationships

Plants of *S. clavicorona* usually consist of only a few large stems, generally between six and 10 of them, but occasionally very large specimens up to 500 mm in diameter are found. The stems may reach 50 mm thick (including the teeth) and are by far the most robust in the genus. They are subtly mottled with purple (particularly if kept in a sunny spot) rather after the manner of *Stapeliopsis neronis* and this phenomenon is otherwise known in *Stapelia* mainly in plants of *S. hirsuta* from the sandstone mountains of the south-western Cape. The tubercles on the stems start off soft and tipped with a small but quite broad leaf-rudiment which soon falls off. They gradually become covered with a pale,

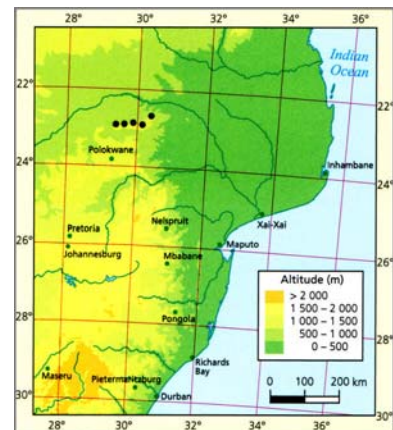


Fig. 15.167. Distribution of *Stapelia clavicorona*.

corky, greyish layer which can eventually form an almost continuous greyish covering along the angles. The tubercles are also unusual in that the leaf-rudiment lies more towards the middle of the tubercle relative to the axis of the stem rather than at the top, which is more typical for *Stapelia*.

In contrast to the robust stems, the flowers of *S. clavicorona* are relatively small and they are usually around 50 mm in diameter. They emit a rather unpleasant excrement-like or urine-like smell. From near the tips of the lobes more or less right to the centre, the corolla is covered with low, transverse ridges that become roughly concentric circles on the united part. The corolla is completely flat except for a very short tube in the centre around the base of the gynostegium and it has short, relatively broad lobes. On the inside it is glabrous except for slightly clavate, vibratile cilia along the margins of the lobes and a dense cluster of somewhat worm-like, downward-pointing hairs which fill up the tube. Flies have been found to lay their eggs among these small hairs in the tube and sometimes the area between the gynostegium and the corolla tube has been seen to be full

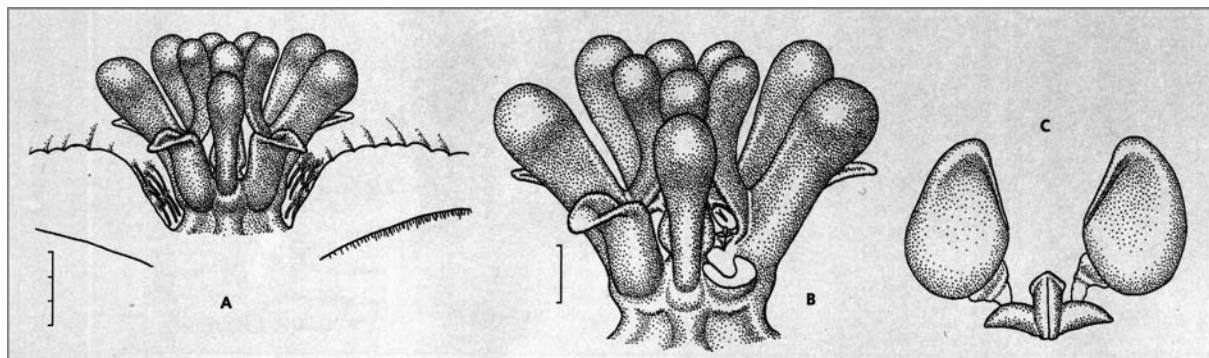


Fig. 15.168. *Stapelia clavicorona*. A, side view of centre of dissected flower. B, side view of gynostegium with one outer corona lobe removed. C, pollinarium. Scale bars: A, 3 mm; B, 1 mm; C, 0.25 mm (at A). Drawn from PVB 7003, near Soutpan, north-western Soutpansberg.



Fig. 15.169. *S. clavicornata*, PVB 7003, near Soutpan, north-western Soutpansberg.



Fig. 15.170. *S. clavicornata*, PVB 6575, Wyllies Poort, central Soutpansberg.

of small, writhing maggots that have hatched from these eggs.

In the centre of the flower there is a dark, almost black gynostegium. This consists of narrow, channelled outer lobes with recurved tips which are not particularly unusual. However, the inner corona, with its five pairs of clavate horns is unlike anything else in *Stapelia* and is reminiscent of species such as *Tromotriche herrei*. Each lobe is flattened towards the base and then rises in the centre into a very swollen, clavate tip. Behind each of them is a large dorsal process (larger than the lobe itself) which is laterally flattened towards the base and, again, very swollen and clavate towards the tip. These lobes are not brightly shiny but nevertheless glisten somewhat and, when viewed under a microscope, are seen to be covered with large cells whose outer walls are shiny and raised into a rounded dome. The outer lobes do not have these swollen cells, being dull by comparison and not glistening at all.

The stout stems and robust pedicels suggest that, despite the relatively small and almost glabrous flowers, this species is most closely related to those with large flowers.



Fig. 15.171. *S. clavicornata*, PVB 7003, near Soutpan, north-western Soutpansberg.

History

Stapelia clavicornata was first collected in January 1931 by Jan J. van Nieuhuys at the northern end of Wyllie's Poort on steep, rocky slopes. Until recently, all recorded collections had been made in this vicinity but it is now known to be considerably more widely distributed.

Probably all the plants in cultivation emanate from Wyllie's Poort. Not only is it extraordinary the extent to which plants of this species have been removed from this place but it is also amazing that no one has attempted to propagate it from cuttings and seed, which is relatively easy in both cases. This lack of propagation is particularly disappointing as it appears that on several occasions substantial numbers of plants have been removed from the wild ostensibly for the purpose of propagation, without anything coming of such initiatives. Nevertheless, it still occurs in this area, if in possibly rather reduced quantities.

26. *Stapelia pillansii*

Stapelia pillansii N.E.Br., *Gard. Chron.* Ser. 3, 35: 242 (1904).

Gonostemon pillansii (N.E.Br.) P.V.Heath, *Calyx* 1: 18 (1992).

Lectotype: South Africa, Cape, near Matjiesfontein, N.S. Pillans 38 (BOL).

S. pillansii var. *attenuata* N.E.Br., *Fl. Cap.* 4 (1): 958 (1909).

Gonostemon pillansii var. *attenuatus* (N.E.Br.)

P.V.Heath, *Calyx* 3: 8 (1993).

Type: South Africa, Cape, Wittepoort, N.S. Pillans 671 (BOL).

S. pillansii var. *fontinalis* Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1145 (1937).

Gonostemon pillansii var. *fontinalis* (Nel) P.V.Heath, *Calyx* 1:18 (1992).

Type: Cape, Matjiesfontein, *Austin sub PRE 50789* (PRE).

Succulent forming clump 150 mm-1 m diam. **Stems** 50-120 (-200) mm long, 10-20 mm thick, decumbent with very shortly horizontal base, shortly pubescent, green suffused with red (not mottled); **tubercles** 2-3 mm long, widely spaced along stem and very obscure, obtusely conical, joined into 4 broadly obtuse angles along stem and stem $\pm$ roundedly square in cross-section; **leaf-rudiments** 1.5-3.0 mm long. **Inflorescences** pubescent, 1-2 per stem near base, each with 1-3 flowers opening in gradual succession on short stout peduncle < 5 mm long with few deltid bracts 1-2 mm long; **pedicel** 20-50 mm long, 4-5 mm thick, purplish, spreading and holding flower facing horizontally; **sepals** 8-10 mm long, 3 mm broad at base, narrowly lanceolate, acute, purplish to green. **Corolla** 150-210 mm diam., $\pm$ rotate; outside dark red-purple with 5 or more darker longitudinal veins on each lobe; inside smooth or finely transversely rugulose, dark red to maroon suddenly becoming yellow towards base of tube, glabrous; **tube** $\pm$ 10 mm long, 20 mm broad, containing $\pm$ whole gynostegium, pentagonal, widening gradually towards mouth which is $\pm$ at base of lobes, corolla thickened (to 2.5 mm) especially towards middle of tube; **lobes** 70-95 mm long, 15-20 mm broad at base, spreading sometimes with reflexed tips, ovate-acuminate and often attenuating into slender twisted tails, flat towards base becoming convex after about 20 mm above from revolute margins, margins in lower half with vibratile slender purple cilia 2-3 mm long. **Corona** $\pm$ 9 mm tall, $\pm$ 9-12 mm broad, raised on obtusely pentagonal stipe 1-2 mm long, shiny blackish purple becoming bright yellow towards base and on stipe; **outer lobes** 4-5 mm long, 1.5-2.5 mm broad, ascending and then spreading, $\pm$ rectangular to oblong, obtuse to $\pm$ deltoid at apex or dentate, slightly to deeply channelled down centre; **inner lobes** 6-8 mm long, adpressed to backs of anthers then connivent-erect and widely spreading-recurved above, dorsoventrally flattened towards base, in upper half becoming flat to slightly channelled inside and dorsally keeled, with broad obtuse laterally flattened ascending-spreading dorsal wing variably fused to but shorter than lobe, sometimes with further lobule at base.

STAPELIA PILLANSII

Distribution and habitat

Stapelia pillansii has a somewhat limited distribution along the northern side of the Little Karoo and south-western Great Karoo from near Pieter Meintjies siding to Laingsburg and then southwards to Kareevlakte and Ladismith.

Specimens are found on the northern slopes of low shale or tillite hills, where they grow under short karroid bushes or between rocks. They are rarely common.



Fig. 15.173. *S. pillansii*, Nagel 94, north of Matjiesfontein (photo: W.R. Liltved).

Diagnostic features and relationships

Plants of *S. pillansii* may reach a very large size (and presumably a considerable age too) and some clumps up to 1 m in diameter have been seen. The stems have very rounded angles, with hardly any groove between the angles, and the tubercles are widely separated and obscure. This is quite distinctive when compared with stems of *S. hirsuta* but is similar to those of *S. rufa*. Both these species are sometimes found together with *S. pillansii*. While *S. hirsuta* is quite easily seen to be different, since the stems have a different colour and a deeper, broadly concave groove between the angles, in *S. rufa* flowers may be necessary to separate them.

The flowers of *S. pillansii* are quite spectacular. Even the bud, with its long beak made up of the slender, slightly spiralling lobes, is remarkable. When this opens, the lobes spread out to produce a flower that may reach 210 mm in diameter. In some cases they fold back behind the flower but they often spread out to this full size against the plant. The lobes are about 18 mm across at the base and, after about 20 mm, begin to narrow (mainly by the folding back of the margins at this stage) to form long, slender tails. The inner surface of the corolla is a rich, velvety dark red to dark maroon which suddenly changes to yellow in the base of the small tube. Plants with entirely yellow flowers have occasionally been collected around Matjiesfontein (the former var. *fontinalis*) but none of these seem to have been gathered recently. Rather unusual for *Stapelia* is the fact that the surface inside is more or less devoid of transverse ridges. A few are indeed present but they are faint and confined mainly to the edges of the lobes. The lobes are fringed with slender, vibratile cilia along their margins but otherwise

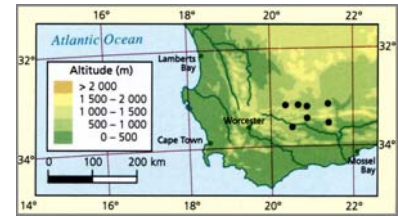


Fig. 15.172. Distribution of *Stapelia pillansii*.

the inside of the flower is without hairs.

The rather shiny, mostly dark corona has the usual structure except for the intermittent presence (even on one flower) of a small ascending lobule at the base of the broad, dorsal wing of the inner lobes. The inner corona lobes generally spread quite strongly towards their tips and their dorsal horn is also somewhat spreading. The two are joined for a very variable length and Leach (1985) illustrated cases where they were almost completely fused, which is not the case in the specimen illustrated here.

As emphasised by Leach (1985), *S. pillansii* is not closely allied to the other species that occur in its vicinity (*S. engleriana*, *S. hirsuta* and *S. rufa*) but rather to *S. schinzii* from Namibia and southern Angola. The two species share the large flowers with similar colouring, as well as the long, slender corolla lobes and similar coronas. They differ mainly in that the almost glabrous stems of *S. schinzii* are usually mottled with purple and have the tubercles joined into (mostly) quite thin wings along them so they are not rounded, the leaf-rudiments are longer (4-5 mm) and the corolla is finely and densely rugulose all over the inside (though this is lacking in var. *bergeriana*, where the inside of the corolla is smooth and very shiny).

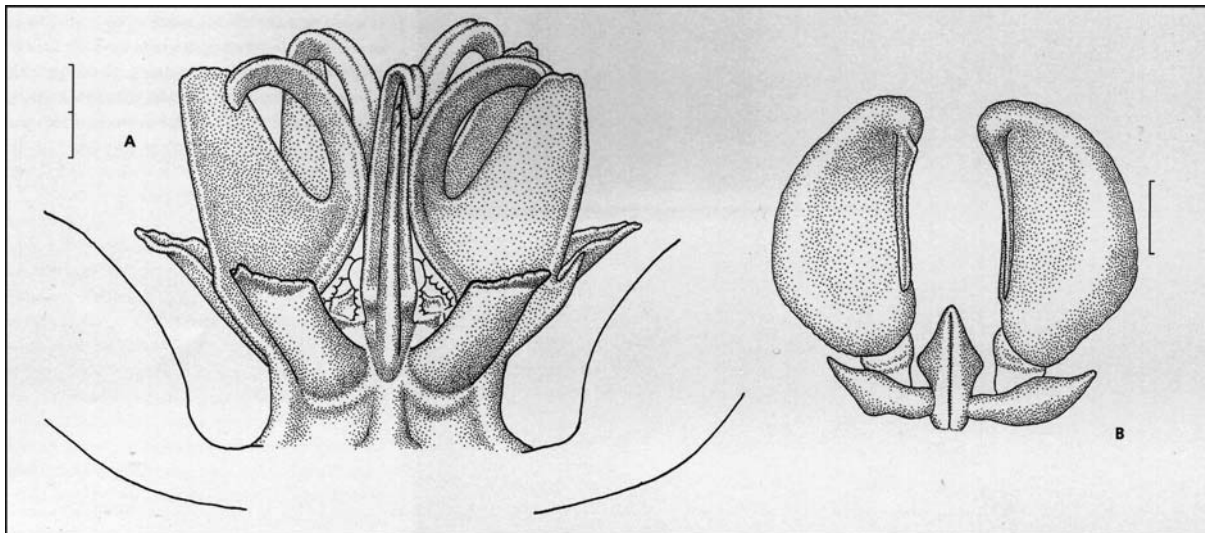


Fig. 15.174. *Stapelia pillansii*. A, side view of gynostegium. B, pollinarium. Scale bars: A, 2 mm; B, 0.25 mm. Drawn from PVB 3644, north-west of Ladismith.

History

Stapelia pillansii was discovered by N.S. Pillans in October 1900 near Matjiesfontein. Apart from the many collections made in this area,

most of which were made in the vicinity of the former Karoo Garden at Whitehill (just east of Matjiesfontein), this species has been collected relatively rarely.



Fig. 15.175. *S. pillansii*, PVB 3644, north-west of Ladismith.



Fig. 15.176. *S. pillansii*, hort. De Kock, yellow-flowered plant known at one stage as 'var. fontinalis' (photo: D. de Kock).

27. *Stapelia schinzii*

Stapelia schinzii A.Berger & Schltr., *Vierteljahrsschr Naturf. Ges. Zürich* 53: 491 (1908).
Gonostemon schinzii (A.Berger & Schltr.) P.V.Heath, *Calyx* 1:18 (1992).
Type: Namibia, Hereroland, near Okomita, Dinter 450 (Z, holo.; PRE, iso., photo only).

Spreading succulent forming loose clumps 150 mm to 1 m diam. **Stems** 30-100 mm long, (5-) 7-20 mm thick, decumbent to ± creeping, slender to stout, ± glabrous, uniformly purplish to green or grey mottled with purple (especially between angles); **tubercles** 1-3 mm long, obscure to strongly deltoid, joined into 4 usually wing-like angles along stem between which stem concave; **leaf-rudiments** 1.5-6.0 mm long. **Inflorescences** very shortly pubescent to ± glabrous, 1 per stem mainly towards base (but sometimes nearly apical), with 1-3 flowers developing in gradual succession on short peduncle up to 10 mm long; **pedicel** 15-60 mm long, 3-6 mm thick, usually spreading to ascending; **sepals** 6-8 mm long, 2.0-2.5 mm broad at base, ovate-lanceolate, acute. **Corolla** 70-220 mm diam., rotate; outside very shortly pubescent, green to reddish with 1-3 darker raised veins running down each lobe; inside finely and densely transversely rugulose (rarely shiny and smooth) becoming smooth near mouth of tube, reddish purple to greenish yellow often becoming yellowish towards tips of lobes, glabrous; **tube** 2-4 mm deep, pentagonal, broadly funnel-shaped and closely adpressed to base of gynostegium, corolla much thickened around mouth; **lobes** 50-90 mm long, 13-20 mm broad at base, spreading, ovate-acuminate to caudate, with margins near base somewhat raised so concave but above this convex with margins recurved, margins in lower half (sometimes for whole length) with dense beard of vibratile purple fusi-form to clavate cilia 3-4 mm long. **Corona** ± 11-12 mm tall, ± 8-10 mm broad, raised on stout yellow pentagonal stipe ± 1.5 mm tall, dark purple-red becoming yellow towards base, sometimes wholly purple suffused with yellow towards tips, glabrous; **outer lobes** 3-4 mm long, ascending and spreading, oblong to rectangular or deltoid, acute to apiculate, lightly channelled above; **inner lobes** 6-9 mm long, adpressed to backs of anthers then erect and then divergent or erect and connivent after which somewhat diverging and then usually converging again, dorsiventrally flattened below becoming slightly concave (on outside) or terete above, lanceolate, acute, with broad laterally flattened ascending to erect ovate-acute to oblong and truncate or irregularly dentate dorsal horn fused at base to and slightly shorter than lobe.

Stapelia schinzii is found in Namibia and southern Angola.

Leach (1985: 71) tabulated the differences between *S. schinzii* and *S. pillansii* and pointed out that these two species are close, though they differ in many features. Actually, many of the distinctions that he listed do not hold. Thus, for example, 'tubercle teeth small' (*S. pillansii*) versus 'relatively large' (*S. schinzii*) cannot be used to separate them, especially since the tubercles are very small in some of the forms of var. *schinzii* from southern Namibia and they

Key to the varieties of *S. schinzii*

- | | |
|---|-----------------------------|
| 1. Stems decumbent, mottled with purple on green | 2. |
| 2. Corolla 70-80 mm diam., inside smooth, shiny | 27b. var. <i>bergeriana</i> |
| 2. Corolla 100-220 mm diam., inside covered with fine transverse ridges, dull | 27a. var. <i>schinzii</i> |
| 1. Stems prostrate with ascending apices, uniformly purplish or green | 27c. var. <i>angolensis</i> |

STAPELIA SCHINZII

are always small in var. *angolensis*. Similarly, he maintained that the leaf-rudiments in *S. schinzii* were 5 mm long whereas in *S. pillansii* they were 3 mm long but in fact in *S. schinzii* they may be as short as 1.5 mm long. I have also found that the outside of the corolla is pubescent in both, though this pubescence is very fine in *S. schinzii* and more coarse and clearly visible in *S. pillansii*. In general, the difference in the pubescence in many parts seems to provide the main distinction between them: *S. pillansii* is quite clearly pubescent on both the stems and the inflorescence whereas in *S. schinzii* the stems appear to be glabrous (though they are actually papillate, as one can see in fig. 18 F) and the inflorescence is only very shortly pubescent. In *S. pillansii* the inside of the corolla is almost smooth but not shiny. In *S. schinzii* it is densely and finely rugulose, except in var. *bergeriana* where it is practically smooth and shiny.



Fig. 15.178. *S. schinzii* var. *schinzii*, Bläskrantz, north of the Naukluft, Namibia, in habitat, March 1993.

27a. *Stapelia schinzii* var. *schinzii*

Stems 7-20 mm thick, decumbent, mottled with purple on green. **Corolla** 100-220 mm diam.; inside covered with fine transverse ridges and somewhat dull. **Inner corona lobes** erect beyond anthers and connivent after which somewhat diverging and then usually converging again, with usually erect dorsal horn.

Distribution and habitat

Var. *schinzii* is known only in Namibia, where it is widespread and relatively well documented. Here it grows mainly east of the Namib Desert. It has been recorded from parts of Ovamboland and the southern Kaokoveld around Opuwa southwards for most of the length of the country to Helmeringhausen, Aus and near Witpütz as well as near Karasburg. It extends further eastwards, mainly in the region around Tsumeb and Grootfontein, but further spreading towards the east seems to be curtailed by the Kalahari sands in this area. It is not known to occur in Botswana.

Specimens are mostly associated with stony flat areas or calcrete patches, sometimes with shallow sand overlying calcrete. Plants grow in the open or among scattered bushes and trees, often at the base of small trees of *Acacia tortilis* or *A. nebrownii* or shrubs of *Catophractes alexandrii*, the driedoring (*Rhigozum trichotomum*), or *Calicorema capitata*.

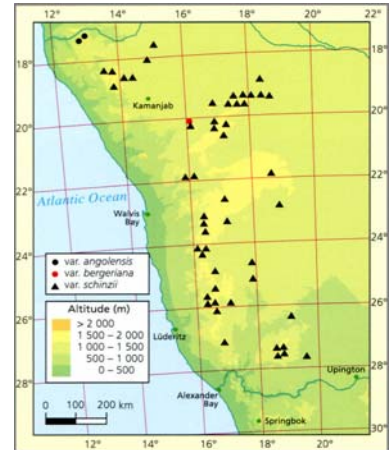


Fig. 15.177. Distribution of *Stapelia schinzii* in southern Africa.

Diagnostic features and relationships

Plants of var. *schinzii* are often large and may spread for up to 1 m. The stems are usually robust and erect above a short horizontal base. They are strongly 4-angled and mottled with purple on green or grey. They are always glabrous to the naked eye, though in fact they are finely papillate under the microscope (fig. 18 F). Right in the south of Namibia, from Bethanie to Helmeringhausen and southwards into the

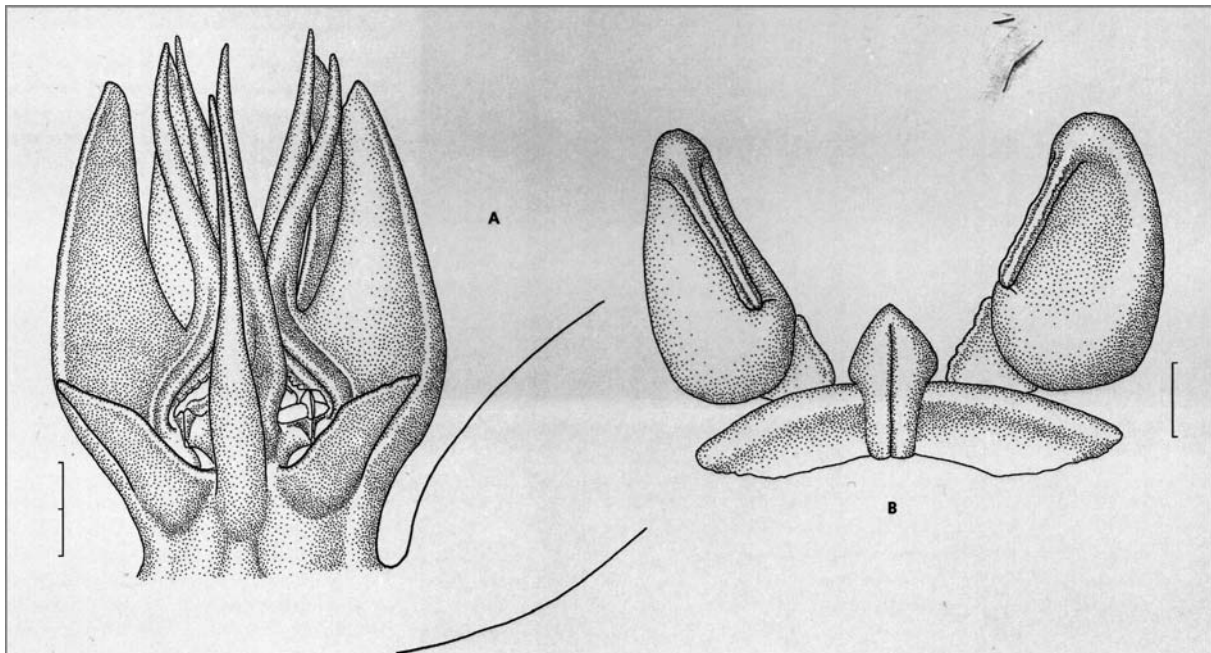


Fig. 15.179. *Stapelia schinzii* var. *schinzii*. A, side view of gynostegium. B, pollinarium. Scale bars: A, 2 mm; B, 0.25 mm. Drawn from PVB 4135, east of Grootfontein, Namibia.

Tiras Mountains, the stems are very much smaller and more slender (often only 5–7 mm thick) and the angles on them are also rather more rounded. Flowers from this area are, however, no different from those of plants with larger stems.

Among all the species of *Stapelia* in Namibia, *S. schinzii* has by far the largest flowers and these may be anything between 100 and 220 mm in diameter. They are dark red-dish purple to greenish yellow and have long lobes which taper gradually into fine tails. The inside is completely without hairs and is covered densely with fine transverse ridges. These ridges become denser and more regular below the bases of the lobes and finally disappear near the corona. The centre of the flower is not completely flat but has a very shallow, funnel-like area outside the tube around the base of the gynostegium. Along the edges of the lobes, particularly towards the base, there are large numbers of vibratile cilia which are usually narrowly fusiform. These are generally conspicuous near the base of the lobes where their margins are not folded back out of sight.

In var. *schinzii* the inner corona lobes have a graceful curvature above the centre of the flower, often arching slightly outwards and then towards one another again. Their dorsal horn tends to be erect with a slightly incurved apex.



Fig. 15.180. *S. schinzii* var. *schinzii*, Bläskrantz, north of the Naukluft, Namibia, in habitat, March 1993. Pale flowers like this occur sporadically over most of the distribution.

History

Var. *schinzii* was discovered by Hans Schinz in 1886. According to Berger (1910), Schinz collected it at Lake Ngami in Botswana and it was also recorded from Lake Ngami by Eduard Fleck in May 1886 (material in Z). As Leach (1985) pointed out, however, it has never been recorded again anywhere in Botswana and it is much more likely that Schinz gathered it

somewhere in Namibia. On this expedition he travelled from Aus in the south to Olukonda in Ovamboland, then to Lake Ngami and then back via Grootfontein and Omaruru to Walvis Bay. He is bound to have encountered this fairly common species somewhere in this area. Similarly Fleck covered much territory in Namibia before reaching Lake Ngami and probably also collected this *Stapelia* somewhere in Namibia.



Fig. 15.181. *S. schinzii* var. *schinzii*, PVB 5570, Kaoko Otavi, Namibia, in habitat, February 1993. The characteristic mottling of the stems may be seen here.

STAPELIA SCHINZII



Fig. 15.182. *S. schinzii* var. *bergeriana*, PVB 1998, north of Outjo, Namibia.

27b. *Stapelia schinzii* var. *bergeriana*

Stapelia schinzii var. *bergeriana* (Dinter) L.C.Leach, *Excelsa Taxon. Ser.* 3: 74 (1985).

Stapelia bergeriana Dinter, *Neue Pflanzen Deutsch-SWAs.*: 51 (1914).

Gonostemon schinzii var. *bergerianus* (Dinter) P.V.Heath, *Calyx* 1:18 (1992).

Lectotype: Namibia, Dinter 2697 (SAM).

Stems 7-20 mm thick, decumbent, mottled with purple on green. **Corolla** 70-80 mm diam.; inside smooth, shiny.

Var. *bergeriana* is vegetatively indistinguishable from var. *schinzii*. It differs from var. *schinzii* in that the inside of the corolla is smooth and shiny, rather than finely rugulose and somewhat dull. The flowers are also rather smaller than is usual for var. *schinzii* in that region. Leach (1985) seems to have been hesitant to recognise this taxon at all and felt that it was perhaps merely an aberrant form of var. *schinzii*, a possibility that is made more likely by the fact that it is extremely rare. He mentioned in this context that other species are known in which the inside of the corolla is normally rugulose but occasional forms are found which are almost smooth inside, for example in *S. kwebensis* and *S. surrecta*.

History

Var. *bergeriana* was collected by Kurt Dinter while on an expedition in northern and central Namibia but he did not note down when or where it was collected, taking it to be the usual *S. schinzii*. When it began to flower in his garden in November 1912, he recognised it as new and named it after his friend Alwyn Berger of La Mortola. It has only been gathered once

since (PVB 1998) and this is illustrated here. This collection was made in December 1979 about 8 km north of Outjo and plants were found under trees in flat areas between dolomite hills. There is no evidence to suggest that this variety is anything more than a smooth- and small-flowered sport, but for the present it is maintained at varietal level.



Fig. 15.183. *S. schinzii* var. *angolensis*, PVB 5583, Otjipemba, Namibia. Plant with shiny flowers very similar to those of var. *bergeriana*.

27c. *Stapelia schinzii* var. *angolensis*

Stapelia schinzii var. *angolensis* Kers, *Bot.*

Notiser 122:176 (1969).

Gonostemon schinzii var. *angolensis* (Kers) P.V.Heath, *Calyx* 1: 18 (1992).

Type: Angola, Mocamedes Distr., 10 km north-east of Vila Arriaga, 3 May 1968, Kers 3441 (S).

Stems 5-10 mm thick, prostrate with ascending apices, uniformly purplish or green. **Corolla** 80-140 mm diam.; inside covered with fine transverse ridges or somewhat shiny. **Inner corona lobes** erect beyond anthers and then slightly to widely divergent, with usually ascending dorsal horn.

Distribution and habitat

Var. *angolensis* is known in southern Angola in the Chela Mountains. In Namibia it is only found in the northernmost part of the Kaokoveld, where the vegetation is, in many respects, more similar to that of southern Angola than to the rest of Namibia. Plants have been recorded along the Kunene River, in the Baynes Mountains and in the valley near Otjipemba.

In the Baynes Mountains var. *angolensis* is not uncommon in some areas and plants were found growing in very shallow soil in crevices in large outcrops of rock and on ledges along the edges of cliffs, usually completely in the open but sometimes among *Xerophyta* shrublets. Kers (1969) also found it in shallow soil on low, dry outcrops of rock on the lower slopes of the Chela Mountains.

Diagnostic features and relationships

This variety differs from the typical mainly by the more loosely spreading and sometimes almost prostrate habit of the stems. They are also considerably thinner than those of var. *schinzii* as it is found in northern Namibia (thin-stemmed forms of var. *schinzii* are, however, more common in southern Namibia) and have more rounded and thicker angles along them. In var. *angolensis* the stems are uniformly purplish or greenish and lack the mottling of purple on grey that is typical of var. *schinzii*.



Fig. 15.184. *S. schinzii* var. *angolensis*, PVB 7999, Baynes Mountains, Namibia, with more shiny flowers than in the next picture.

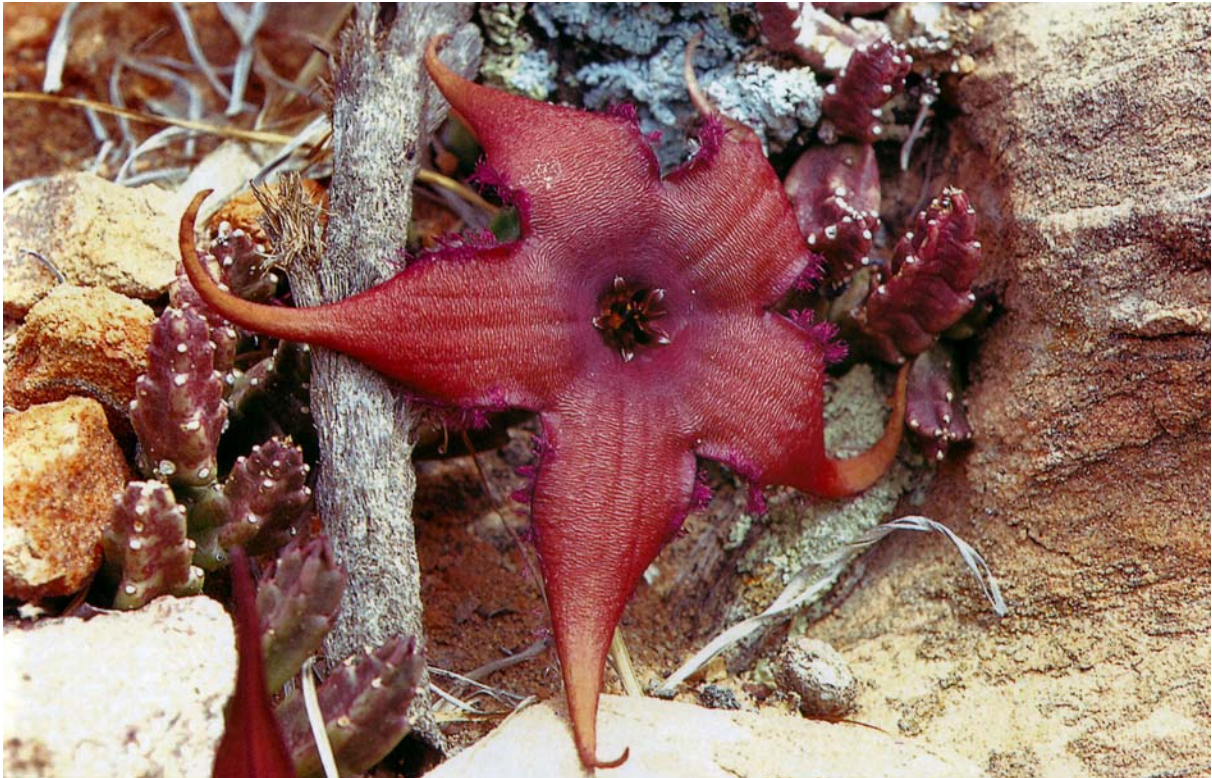


Fig. 15.185. *S. schinzii* var. *angolensis*, PVB 7999, Baynes Mountains, Namibia. Plant wedged among old *Xerophyta* stumps in crevices in rocks just above large cliffs, December 1999.

The flowers in var. *angolensis* are a little smaller than is usual in var. *schinzii* and seem usually to be somewhat shiny, though they are very variable in this regard. They also show a similar range of colour to what is known in

var. *schinzii* and some flowers are distinctly yellowish on the lobes while others are more brownish.

In var. *angolensis* the inner corona lobes are ascending to quite widely spreading and are

sometimes dorsally canaliculate. Their dorsal horn always seems to be slightly spreading and may sometimes be canaliculate on the rear. In some plants the tips of the lobes become pale yellowish.

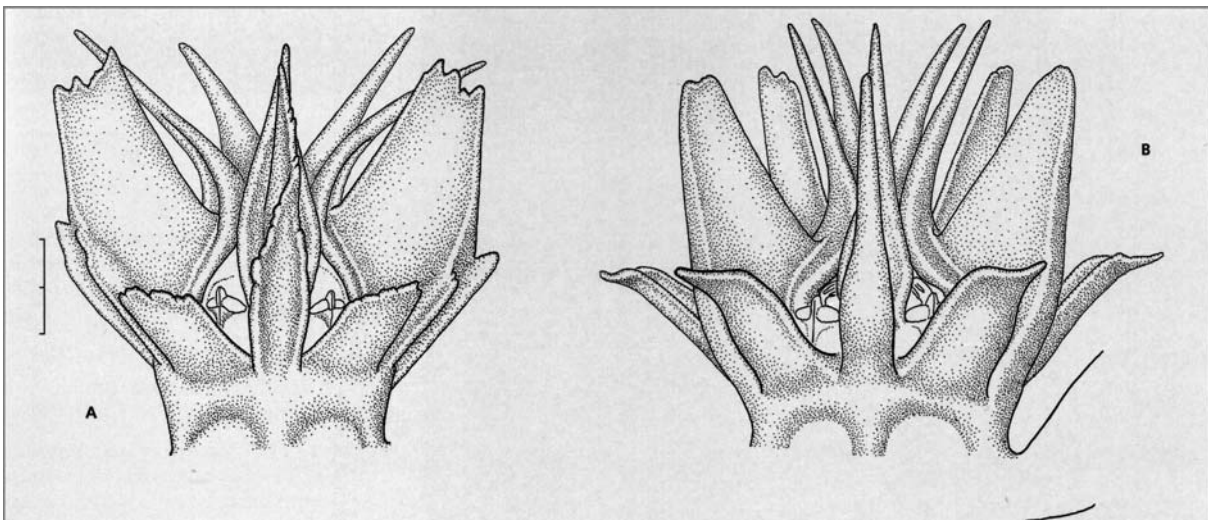


Fig. 15.186. *Stapelia schinzii* var. *angolensis*. A, B, side view of gynoecium. Scale bars: A, B, 2 mm (at A). Drawn from A, PVB 7999, Baynes Mountains, Namibia; B, PVB 5583, Otjipemba, Namibia.

STAPELIA REMOTA

History

The first record of this variety was made in March 1923 by the marine biologist Keppel Harcourt Barnard. He made a collection of it in northern Namibia at a place called 'Nanquali Rapids', which lies somewhere along the banks of the Kunene River downstream from

the Ruacana Falls but cannot be located with certainty today. It was gathered in Angola near Vila Arriaga for the first time in 1956 by the Portuguese botanist Eduardo J. Mendes and was described from plants found by Lars Kers in much the same area in the Chela Mountains of southern Angola.



Fig. 15.187. *S. schinzii* var. *angolensis*, PVB 7999, Baynes Mountains, Namibia. A large plant cascading down rock outcrops near the base of some large cliffs, December 1999.

28. *Stapelia remota*

Stapelia remota R.A.Dyer, *Bothalia* 12: 632 (1979).
Gonostemon remotus (R.A.Dyer) P.V.Heath, *Calyx* 1:18(1992).

Type: Namibia, ? Baynes Mountains., *Steenkamp*
sub PRE 57257 (PRE).

Small succulent forming dense clump. Stems 50-150 mm long, 10-15 mm thick, decumbent with short horizontal base, $\pm$ glabrous, green to grey-green; **tubercles** 1-3 mm long, widely spaced along stem, obscure, laterally flattened and joined into 4 continuous narrowly obtuse angles along stem with stems square to slightly concave-sided; **leaf-rudiments** < 1 mm long. **Inflorescence** finely pubescent, 1 per stem near base, with 1-3 flowers opening in gradual succession on peduncle up to 5 mm long with few slender bracts 1-2 mm long; **pedicel** 6-12 mm long, 1 mm thick, spreading and holding flower facing outwards; **sepals** 3-4 mm long, 1 mm broad at base, lanceolate, acute. **Corolla** 15-20 mm diam., $\pm$ turban-shaped; outside pale green with 1-3 darker longitudinal veins on each lobe; inside somewhat shiny, dark red to maroon becoming yellowish towards tips of lobes, smooth except for irregularly spaced low rounded multicellular papillae around mouth of tube and base of lobes, tube covered with small dark purple clavate unicellular papillae spreading beyond mouth in patch opposite sinuses of lobes, otherwise glabrous; **tube** $\pm$ 3 mm long, 8 mm broad, bowl-shaped, strongly pentagonal, with corolla somewhat thickened around mouth; **lobes** $\pm$ 5 mm long, 7 mm broad at base, reflexed behind corolla, broadly ovate, acute, convex above from reflexed margins, with dense fringe of rigid cylindrical to slightly clavate maroon hairs up to 3 mm long (each arising from small papilla) along margins except near tip. **Corona** $\pm$ 5 mm tall, $\pm$ 5 mm broad, raised on short pentagonal stipe $\pm$ 1 mm long, dark red-brown; **outer lobes** 3 mm long, 1 mm broad, ascending, oblong and widening towards apex, truncate to slightly tridentate, channelled above from incurved sides, yellow at base; **inner lobes** 4.5 mm long, adpressed to backs of anthers then connivent-erect then widely recurved, dorsiventrally flattened at base (but narrower than anthers), then slender and terete with very slightly swollen apex, with ascending linear laterally flattened obtuse dorsal wing $\pm$ 3.5 mm long.

Distribution and habitat

Stapelia remota is apparently known from a single locality in the western corner of the Baynes Mountains in the Kaokoveld, Namibia. Here it is supposed to have been found growing in crevices on a dolomite cliff together with *Aloe corallina* at an altitude of between 1 500 and 1 900 m.

Diagnostic features and relationships

The stems of *S. remota* are most unusual. They have especially narrow and small angles, between which the surface is hardly concave at all so that in cross-section the stem is more or less square. They are glabrous to the naked eye and feel smooth as well. Actually they are

finely pubescent but this is only visible under a microscope.

Flowers are borne near the base of the stem and face outwards. They are relatively small, shiny inside and dark red, emitting an unpleasant, excrement-like odour. In the centre there is a small, strongly pentagonal tube which is thickened around its mouth. The lobes begin a little beyond the mouth of the tube and are bent back strongly behind it so that the flowers have somewhat of a button-like shape. The inside of the tube is quite densely covered with small, clavate papillae, each of which consists of a single enlarged cell (fig. 28 H). Beyond the crust of these papillae and onto the bases of the lobes, the surface is shiny but has scattered, low, many-celled papillae that give it a pustulate appearance. There are no hairs except for a fringe of quite long, shiny, cylindrical to clavate ones along the margins of the lobes. These are firmly fixed and not at all vibratile.

The corona is not unusual for *Stapelia*, with narrow, strongly channelled, ascending outer lobes and inner lobes which become clavate towards the tips and are nearly equaled by their laterally flattened dorsal horn.

The flower of *S. remota* resembles that of *S. engleriana* in the manner in which the corolla lobes are folded back and in the long, terete inner corona lobes. These even mildly suggest a relationship to *Tromotriche revoluta*. However, the stems are more suggestive of some of the 'glabrous' forms of *S. hirsuta*. The small papillae inside the corolla tube are similar to (though smaller than) those found in *S. flavopurpurea*, but the mound-like papillae outside the tube are not matched anywhere else in *Stapelia*.

History

According to records kept at the National Herbarium in Pretoria (PRE), *S. remota* was found inadvertently by P. Steenkamp in July



Fig. 15.188. *S. remota*, Steenkamp sub PRE 57257, ? west of Baynes Mountains, Namibia.

1976 while he was collecting *Aloe corallina* on cliffs on Okakora, west of the Baynes Mountains in the Kaokoveld of Namibia. It was claimed that a small seedling of a stapeliad was discovered later among the roots of one of these aloes. This plantlet was carefully tended and, when it flowered, it was described as *S. remota*.

However, some doubt must be expressed regarding the origin of this plant. I have spent considerable effort on three separate occasions trying to relocate this species and, while this has had numerous other interesting results (such as the discovery of *Baynesia lophophora*), *S. remota* has not been relocated in the field. Specimens of *Stapelia* have been found on the cliffs on some of these mountains but they are all *S. schinzii* var. *angolensis*, while *S. kwebensis* has been seen growing at lower altitudes. It is

quite possible that *S. remota* is of extremely local occurrence and has been missed but, in my experience, this would be very unusual, especially in such an undisturbed area. A further curious circumstance is that none of the botanists present when the aloes were collected can recall this stapeliad (O.A. Leistner, pers. comm. 2000; E.G.H. Oliver, pers. comm. 2000). A possibility which must be considered is that this is a hybrid which appeared in cultivation in Pretoria, germinating fortuitously in a pot in which *Aloe corallina* was growing. The peculiar papillae on the corolla, rather than transverse ridges, and the odd papillae in the corolla tube might be evidence for this. Here *S. remota* is treated in detail (and included in the key) but it has not been included in the cladistic analysis as its existence as a species is not established.

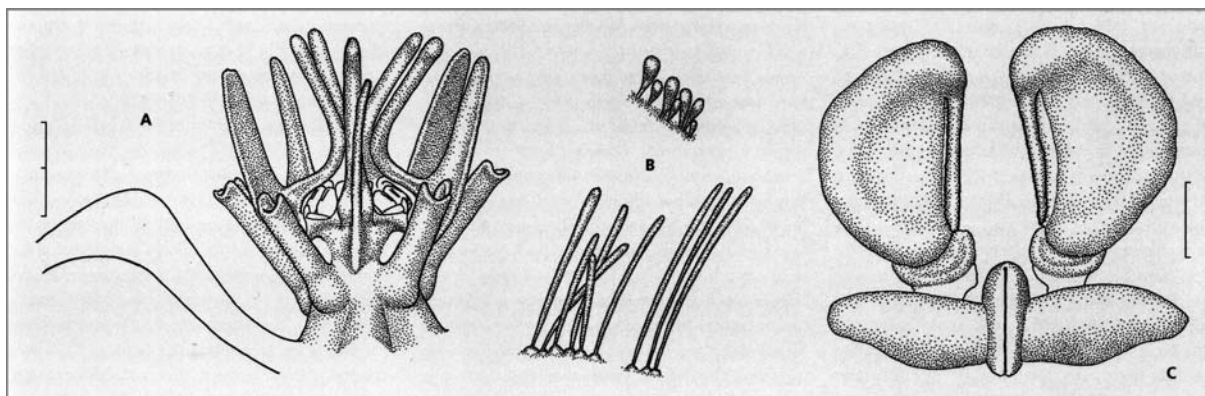
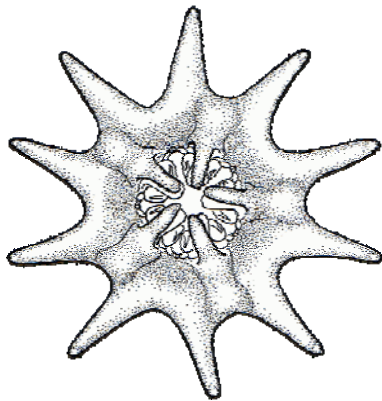


Fig. 15.189. *Stapelia remota*. A, side view of gynostegium. B, papillae inside corolla: above in tube; below along margins of lobes. C, pollinarium. Scale bars: A, 2 mm; B, upper 0.5 mm (at C), lower 1 mm (at C); C, 0.25 mm. Drawn from Steenkamp sub PRE 57257, ? west of Baynes Mountains, Namibia.

16. Stapelianthus



The first species of stapeliad to be discovered on Madagascar was found in January 1918 by Raymond Decary who was the provincial Commissioner of the southern district of the island. This was the very unusual plant described by the French botanist Pierre Choux as *Trichocaulon decaryi* in 1932. Within five years of this first discovery, Decary had found another two, one near Ambovombe and another near Fort Dauphin. The first of these was described by Choux as *Stapeliopsis madagascariensis* in 1931 but, since the generic name had already been used by N.S. Pillans in 1928, *Stapeliopsis* Choux was illegitimate. Once he became aware of this fact, Choux moved this species to a new genus, *Stapelianthus*. In 1934 he described the third species found by Decary as *Stapelianthus decaryi*.

After this, it was some years until Pierre-Rene Montagnac discovered *S. montagnacii* in 1940 near Tuléar and, in 1957, showed flowering specimens of the remarkable *S. insignis* to Bernard Descoings, who was at the time a resident botanist in Tananarive. It is in this area i.e. the south-west and west, where further species have more recently been found.

Stapelianthus has never been accurately defined and this may have led P. Boiteau to describe *S. montagnacii* first as a *Stapelia*, an error which was fairly soon rectified. Subsequent confusion also arose when R.A. Dyer (1965) moved *Stapelia choanantha* to *Stapelianthus* and Leach (1968) followed soon afterwards with *Stapelianthus baylissii*, a species that is rather similar to *S. choanantha*. Both of these are native to the Cape Province in South Africa. Rauh & Wiertel (1968) showed quite clearly that these two species had little in common with the Madagascan species of *Stapelianthus*, but only in 1978 were they moved to *Tridentea* by Leach (Leach 1978b). Once this happened *Stapelianthus* was again restricted to species endemic to Madagascar. Decary's earliest discovery, the peculiar *Trichocaulon decaryi*, was transferred to *Stapelianthus* in 1961, making this the only genus of stapeliad represented on the island. The genus was

recently reviewed by Morat (1994, 1995) and Rauh (1998). Both authors discussed nine species. However, a more recent revision (Bruyns & Klak 2004) has shown that this can be reduced to seven. In this account both morphological and molecular data are used to shed light on the relationships between the species and between *Stapelianthus* and supposedly related genera. It has been found that *Stapelianthus* forms an evolutionary lineage that is quite distinct from the remainder of the stapeliads in Africa. Nevertheless, it is somewhat surprising that even between such distinctive species as *S. pilosus* and *S. arenarius* there is remarkably little variation in the gene-regions examined and that in general there are relatively few characters separating the species. Consequently, the relationships between the species remain largely unresolved and weakly supported. Although the genus remains morphologically difficult to circumscribe, it is defined by its unique corona structure.

Stapelianthus Choux in A.C. White & B. Sloane, Stap., ed. 1:71(1933).

Type: *Stapeliopsis madagascariensis* (Choux) Choux.

Stapeliopsis Choux, Compt. Rend. Hebd. Seances Acad. Sci. Paris 193:1444 (1931), nom. illegit., non Pillans (1928), nec Phillips (1932).

Type: *Stapeliopsis madagascariensis* Choux.

Small spineless non-rhizomatous succulent, forming dense to diffuse mats up to 1 m diam. **Stems** 25-200 (-400) mm long, 3-15 mm thick, procumbent to decumbent, fleshy and firm, glabrous; **tubercles** arranged in 4-8 angles or densely covering the stem, not laterally flattened, each bearing a small leaf-rudiment which soon dries out and falls off, often bullate, without stipular denticles. **Inflorescence** glabrous, 1 per stem near base, of 1-3 (-5) flowers developing in slow succession from peduncle < 2 mm long, with 1-3 deltoid bracts < 1 mm long without lateral teeth; **pedicel** 3-12 mm long, 1-2 mm thick, ascending; **sepals** 2-9 mm long, subulate to lanceolate, acute. **Corolla** 10-35 mm diam., rotate to cylindrical sometimes with prominent shiny annulus; outside glabrous and smooth; inside usually with many conspicuous cylindrical obtuse papillae (very small and few only in *S. insignis*) each with a small apical bristle; **tube** usually just containing gynostegium; **lobes** usually spreading, $\pm$ deltate, with tissue between them folded into spreading often acute lobule, margins eciliate. **Corona** 2.0-6.5 mm tall, 4-8 mm broad, consisting of 2 series arising on staminal tube and partly intergrown, glabrous, very dark red or purple; **outer lobes** 2.5-7.5 mm long, mostly erect from base and spreading towards tips (rarely spreading from base, *S. arenarius*), free usually practically to base, forming cupular structure around central part of gynostegium and mostly considerably exceeding this, dorsiventrally flattened, deeply to shallowly bifid into erect to somewhat recurved narrowly deltoid lobules; **inner lobes** 0.4-1.0 mm long, adpressed to backs of anthers and rarely exceeding them, dorsiventrally flattened, small and inconspicuous, dorsally fused to cup formed by outer corona lobes. **Anthers**



Fig. 16.1. Distribution of *Stapelianthus*.

horizontal to descending on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** D-shaped, insertion-crest twisting from outer edge to dorsal surface, caudicle attached with broad cupular pad to base. **Follicles** erect, terete-fusiform, obclavate, slender, consisting of 2 horns diverging at 30-150°, longitudinally mottled with narrow broken purple stripes, glabrous and sometimes rugulose.

Stems in *Stapelianthus* are procumbent in most species, often with ascending apices. Plants tend to become more erect if they are more exposed to sunlight, so those that are deeply hidden in bushes maintain the most nearly horizontal habit. Only in *S. decaryi* are they decumbent with only a shortly prostrate base.

The stems tend to form dense clumps. In *S. montagnacii* and *S. decaryi* these clumps may exceed 1 m in diameter, while in the other species they are rather smaller (up to 0.3 m). Rhizomatous stems do not occur at all.

In *S. pilosus* the fairly small, conical tubercles are densely packed on the stems and there is no discernible arrangement into angles.

In this species the stems are uniformly green and their surface is smooth. In the others the tubercles are arranged along the stems in 4-8 angles. In *S. arenarius* the angles are not very clear but in the other species the tubercles are joined into low wings along the stems. Here the stems are mottled with purple-brown on a cream to silver-grey or greenish background. In all except *S. decaryi* the surface is bullate, especially towards the edges of the tubercles and this phenomenon is most marked in *S. are-*

nanus. In all species, including *S. decaryi*, the tubercles are broad and somewhat flattened, narrowing abruptly into the leaf-rudiment.

Leaf-rudiments are present in all species, but are always very small. They dry out rapidly but persist as a whitish husk, for a long time in *S. pilosus* and in the others more fleetingly. Initially erect, in all species except *S. pilosus*, the stronger growth of the upper surface of the tubercle pushes the leaf-rudiment finally into a descending position. In *S. pilosus* the tubercle tapers gradually into a slender, filiform, almost cylindrical leaf-rudiment. In *S. decaryi* the leaf-rudiment is narrowly conical and slightly flattened above. In all the other species it is a small, ovate-lanceolate to narrowly deltoid structure that is flat on the upper surface and keeled below and merges into the apex of the tubercle. Stipular denticles are absent.

In *Stapelianthus* the solitary inflorescences arise near the base of the younger stems. Several flowers are borne in very slow succession, usually with only one flower in a given inflorescence opening at a time.

There is a remarkable degree of variation in the geometry of the corolla within this small genus. Here one finds flowers that are nearly flat in *S. arenarius* and are shallowly campanulate in *S. madagascariensis* or more deeply campanulate in *S. montagnacii*. More unusual shapes also exist and the corolla is rotate with a conspicuous annulus in *S. keraudreniae*, bicampanulate in *S. insignis* and deeply tubular in *S. decaryi*.

The flower is neither large nor very small, though it is considerably smaller in *S. pilosus* than in any of the others. While the outside is smooth, the inside is papillate in all species, but there is a remarkable range across the genus in the size of these papillae. In *S. decaryi* the inside is densely covered with stout, columnar papillae, whose apical cell is modified into an acute bristle. In *S. montagnacii*, *S. madagascariensis* and, to a lesser extent *S. pilosus*, the papillae are uniquely long and slender, with a minute apical bristle which is obtuse in *S. madagascariensis* and spherical to cylindrical in *S. montagnacii* (fig. 27 F). In *S. keraudreniae* and *S. insignis* the papillae are very much smaller. In *S. keraudreniae* they are found all over the corolla, with longer ones only towards the edges of the lobes, whereas in *S. insignis* they are located only around the edges of the lobes.

In several species there is a thickening of the corolla around the mouth of the tube but only in *S. insignis* and most noticeably in *S. keraudreniae* does this lead to a definite annulus. In the latter it is also brightly coloured.

The outer corona lobes have a characteristic shape. They are always broad and dorsiventrally flattened, erect to ascending above the base and remain close laterally so as to form the outline of a deep cup, in the base of which

the inner lobes are situated. In *S. pilosus* they are fused for nearly half their length whereas in all the other species they are free nearly to the base. The inner corona lobes are short, adpressed to the anthers and do not usually exceed them. They are joined by a ridge of tissue near their bases to the outer series but have no dorsal horns or projections.

The style-head in *Stapelianthus* is more or less concave above. Situated between the anthers are five high points which are mostly well above the level of the centre. Between these high points there are five lower areas into which the anthers are pressed. These lower areas are usually just below the level of the centre and descend slightly towards the middle before rising abruptly to meet the slight mounds which lie at the centre. The anthers are then usually slightly descending (noticeably so in *S. montagnacii* and *S. insignis*), with the inner corona lobes often also descending towards the centre. The outer edge of the five highest areas (between the anthers) slopes upwards so that the corpuscle is thus also held facing obliquely inwards and this is the case even in *S. pilosus*. The pollinia lie on the region sloping away from this highest area and also usually descend slightly towards the centre.

In *S. pilosus* the pollinia are more or less elliptic and fairly small. In all others the pollinia are medium-sized to large, D-shaped, with the corpuscle widening towards the apex and flanked by long, narrow wings. The caudicle is usually much broadened towards the top with the pollinium attached to the broadest, rather spatulate part. In all species the insertion-crest is attached on the edge at the top of the pollinium, after which it twists around slightly onto the upper surface towards the middle of the pollinium.

In *S. arenarius* the rather slender horns of the foliicles diverge at about 150°, the surface is covered with irregular ridges and is mottled with purple on a paler background. In *S. montagnacii* the horns of the foliicles also diverge at about 150°. However, in this and the other species the surface is smooth and mottled with longitudinal purple lines on a grey background. In the remaining species the horns diverge at 30–60°.

In all seedlings observed the cuneiform hypocotyl is most unusually mottled with purple on a pale creamy green background.

When describing *Stapeliopsis madagascariensis*, Choux (1931) mentioned that the organisation of the flower approaches that of *Caralluma* (with corona as in *C. dependens*) and that the general impression is similar to that of *Stapelia*. White & Sloane (1937) were the first to suggest that *Stapelianthus* is most closely allied to *Huernia*. This view appears to have been reinforced subsequently by the discovery of species such as *S. insignis* and *S. keraudreniae*, which have considerably extended the

range of corolla shapes found in *Stapelianthus*. These new corolla shapes revealed unexpected further parallels with *Huernia*, as was pointed out by Gilbert (1975), and one may see these by comparing flowers of *H. erectiloba* and *S. insignis* and flowers of and *S. keraudreniae*. The inclusion of *S. pilosus* in *Stapelianthus* further substantiated this relationship since, as White & Sloane (1937) already indicated, the remarkable stems of this species are very suggestive of those of *H. pillansii*.

As evidence for the relationship with *Huernia*, White & Sloane mention the 'leafless' stems, their 'appearance' and habit of growing in 'large crowded tufts', the 'small fascicles at the very base of the stems' in which the flowers arise and in the flowers the 'tubular to campanulate shapes, with the inner corolla surface papillate' and the manner in which the 'sinuses between the corolla lobes projected into small intermediate points'. All these features are actually present in a wider range of genera, including *Duvalia*, *Huernia*, *Orbea*, *Stapelianthus*, *Tavaresia* and *Whitesloanea*. There is quite a bit of evidence (Bruyns 2000a) that, amongst modern stapeliads, *Stapelianthus* and *Tavaresia* have the most morphological features in common. Our own research (Bruyns & Klak, 2004), in which a detailed morphological examination of *Stapelianthus* was carried out and molecular data were included, has shown that *Stapelianthus* is difficult to circumscribe morphologically and is defined by the unique bifid outer corona lobes forming a cup-like structure around the gynostegium with small inner corona lobes adpressed to the backs of the anthers and rarely exceeding them. Our molecular data have shown that *Stapelianthus* forms an evolutionary lineage that is distinct from all other stapeliads in Africa. When morphological data are combined with the molecular data, our analyses show that the closest ally is *Tavaresia*.

One rare characteristic that is common to most species of *Stapelianthus* is the bullate surface of the stems. On the African continent this is known only in *Echidnopsis leachii*, the few species of *Rhytidocaulon* and in *Baynesia*. It is, however, a particularly common phenomenon among the asclepiads from Madagascar. It is very evident in various highly succulent species of *Cynanchum* from dry places all over the island and also in several succulent species of *Ceropegia*, both from the arid south-west and elsewhere on the island.

Stapelianthus is endemic to Madagascar and is the only stapeliad genus found there. The seven species grow only in the extreme south and south-west of the island from Fort Dauphin in the east to Morombe in the west. These are the driest parts of the island, in the main receiving less than 400 mm annually, though it appears that the rainfall west of Fort Dauphin, where *S. decaryi* grows, may exceed

STAPELIANTHUS DECARYI

1 000 mm in a year. The distribution of *Stapelianthus* is remarkably poorly documented and only a handful of herbarium specimens has been located. Consequently the distributions plotted on the maps here are not considered to be very reliable.

The most widely distributed species is *S. decaryi*. The next most widely distributed are *S. insignis* and *S. madagascariensis*, while *S. pilosus* and *S. keraudreniae* appear to be the most localised. Species are rarely found growing together (the only recorded cases involve *S. madagascariensis* and *S. pilosus*) and it would appear that the wide variety of different edaphic conditions and soil-types that are present in this part of Madagascar have been a significant force in speciation in the genus.

1. *Stapelianthus decaryi*

Stapelianthus decaryi Choux, *Ann. Inst. Bot-Geol. Colon. Marseille* Ser. 5, 2: 7 (1934).

Type: Madagascar, near Anosy, gneiss rocks on the eastern shore of the Ranofotsy Lagoon, *Decary* (missing).

Lectotype: *Ann. Inst. Bot-Geol. Colon. Marseille* SER. 5, 2: Planche II D.

Stems (10-) 25-100 mm long, 5-15 mm thick, forming dense clumps, decumbent to erect, grey-green to brown mottled with dark brown, surface $\pm$ smooth; **tubercles** flattened-conical, weakly joined into roughly 6 (-8) angles, tapering abruptly into a narrowly conical spreading leaf-rudiment 2-4 mm long and < 1 mm broad which soon withers but persists for a time as a white nearly spine-like husk. **Pedicle** 4.0-8.5 mm long, 1.5-2.0 mm broad, ascending, holding flower facing upwards; **sepals** 3-6 (-7) mm long, 1.5-2.0 mm broad at base, ovate-lanceolate, acuminate, with narrow sometimes slightly recurved tips, green to cream. **Corolla** (10-) 15-23 mm diam., tubular-campanulate; outside cream with fine round maroon spots; inside densely covered in upper half of tube and on lobes (becoming sparser and smaller in lower third of tube) with cylindrical papillae up to 0.6 mm long (usually with red to blackish apex) each tipped with an ascending bristle, cream with fine maroon spots usually becoming uniformly maroon on lower half of tube; **tube** (5-) 10-16 mm long, 6-9 mm broad, cylindrical, usually narrowing slightly towards mouth and widest near base, not thickened around mouth; **lobes** 5.0-8.5 mm long, 4-8 mm broad at base, deltate, acute to acuminate, spreading to reflexed. **Corona** 5.0-6.5 mm tall, 4-6 mm broad, dark maroon, raised on white (with few purple-red spots) pentagonal stipe up to 1.5 mm long; **outer lobes** 4.5-6.0 mm long, erect to slightly spreading, divided to middle or below into slender almost filiform slightly diverging to erect teeth, sometimes with an additional small tooth between them; **inner lobes** $\pm$ 0.6 mm long, deltoid, obtuse, but not usually exceeding anthers.

Distribution and habitat

The most widespread species of *Stapelianthus*, *S. decaryi* is found from near the coast near Fort Dauphin in the east, westwards to Ambovombe and northwards at least to Ihosy and Zazafotsy on the southern edge of the central plateau. There are reports that it occurs as far west as Ampanihy and even Itampolo (H. Petignat, pers. comm. 1994) but this has yet to be confirmed.

The habitat of *S. decaryi* is quite different from that of the other species and it seems mainly to inhabit shallow pockets of soil or leaf-litter on gneiss domes. In the vicinity of Fort Dauphin it is very common and grows on the lower slopes of mountains on black, exposed whalebacks of gneiss, in the company mainly of *Pachypodium horombense*, *Kalanchoe orgyalls* and *Ischnolepis graminifolia*. It is also very common on steep, exposed, black gneiss outcrops around Ihosy where it grows with *Pachypodium rosulatum*, *Kalanchoe orgyalis* and *Euphorbia xylophyloides*, among a host of other succulents. Even further north it was seen near Zazafotsy on flat gneiss outcrops covered scantily with *Xerophyta*, *Aloe intermedia* and *Kalanchoe synsepala*.

Diagnostic features and relationships

Stapelianthus decaryi is most easily recognised when sterile by its almost erect stems that are clustered together into densely packed clumps (fig. 16.5). Very large plants, which may be up to

Key to the species

1. Stems distinctly 4-6 (-8)-angled, tubercle tipped with a conical to narrowly deltoid leaf-rudiment 2.
2. Corolla with cylindrical tube, stems decumbent to erect with smooth surface 1. *S. decaryi*
2. Corolla tube not cylindrical, stems procumbent with bullate surface 3.
3. Corolla $\pm$ rotate 4.
4. Corolla with conspicuous shiny annulus, inside greenish to dull yellow spotted with wine- to purple-red on lobes 4. *S. keraudreniae*
4. Corolla without annulus, inside white with red-brown spots 3. *S. arenarius*
3. Corolla shallowly campanulate or bicampanulate 5.
5. Corolla bicampanulate, inside smooth except for few small papillae along edges of lobes 5. *S. insignis*
5. Corolla shallowly campanulate, inside covered with conspicuous slender papillae 6.
6. Corolla inside maroon to red on lobes mottled with cream in tube, outer corona lobes bifid in upper third only 6. *S. montagnacii*
6. Corolla inside cream with maroon spots, outer corona bifid at least to middle 7. *S. madagascariensis*
1. Stems densely covered with small conical tubercles, each tipped with a fine recurved hair-like leaf-rudiment 2. *S. pilosus*



Fig. 16.2. Distribution of *Stapelianthus decaryi*.

1 m in diameter, are not uncommon. Although the surface of the stems is not as rough as it is in most other species, the stems nevertheless have a similar colouring and, if exposed, they become pale brown with darker mottling. The tubercles are very roughly arranged into six angles along the stems. Each is tipped with a fairly long, slender and spreading leaf-rudiment. This gradually wears off, making the older stems essentially tessellate.

In *S. decaryi* the flowers are erect among

the stems and may be pressed a little out of shape by them. Of all the species, *S. decaryi* has the most tubular flowers. They are extremely variable and in some observed near Ihosy the corolla tube was as short as 5 mm, whereas it is usually around 10-15 mm long. Both the inside and the outside are cream with numerous round maroon spots. Inside the flower these spots coalesce into a solid maroon area in the lower half of the tube. The inside is also covered with relatively short, cylindrical papillae which are

clearly visible to the naked eye and are densest around the mouth of the tube and on the lobes. These are often tipped with a dark patch and a small ascending, apical bristle, and their whole surface is itself finely papillate.

In *S. decaryi* the corona stands on a fairly tall white stipe, well above the base of the tube. The dark maroon outer corona lobes are long and are deeply bifid into slender lobules which are more or less erect. They tower well above the inner lobes.

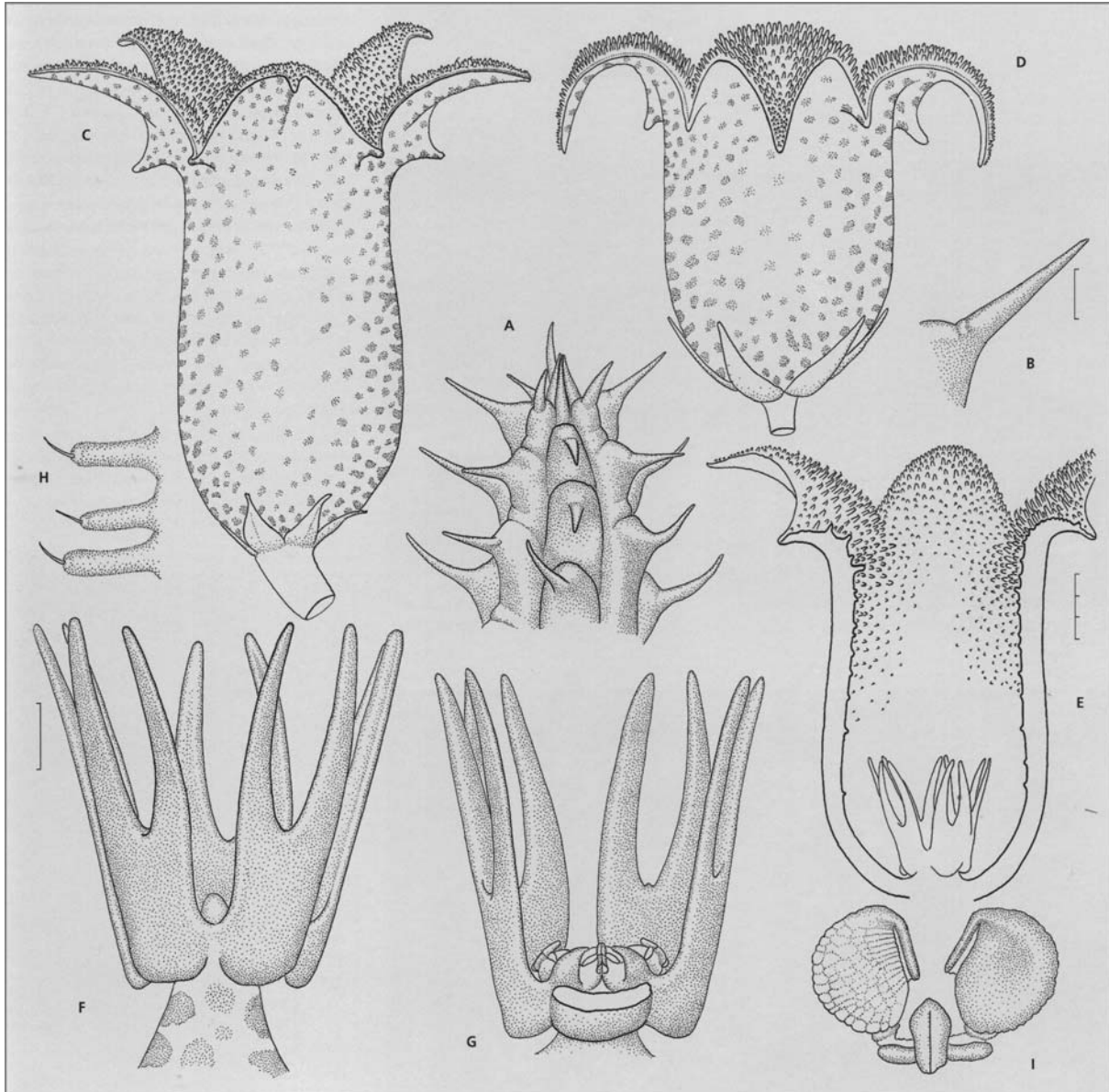


Fig. 16.3. *Stapelianthus decaryi*. A, portion of stem. B, leaf-rudiment. C, D, side view of flower. E, side view of dissected flower. F, side view of gynostegium with tall basal stipe. G, side view of gynostegium with one outer corona lobe removed and with much shorter stipe. H, papillae inside corolla around mouth of tube. I, pollinarium. Scale bars: A, C-E, 3 mm (at E); B, 1 mm; F, G, 1 mm (at F); H, 0.5 mm (at F); I, 0.25 mm (at F). Drawn from A-C, E, G, *hort. De Boer*; D, H, *hort. Oxford*; F, I, *PVB 5960*, near Fort Dauphin, Madagascar.

STAPELIANTHUS PILOSUS

Easily recognised when sterile and still more unmistakable when in flower, *S. decaryi* is probably the species that most clearly exhibits the similarity of *Stapelianthus* to the African genus *Tavaresia*. The stems (although lacking the spines), the shape of the flower, the papillae within the flower and the shape of the corona (in which the lobules of the outer corona lack the pendulous, apical knob of *Tavaresia*) are all suggestive of those in *Tavaresia*.

History

Stapelianthus decaryi was discovered by Raymond Decary in July 1932 at the coast to the west of Fort Dauphin. It was the third species of *Stapelianthus* that he found.



Fig. 16.4. *S. decaryi*, PVB 5960, near Fort Dauphin, Madagascar.



Fig. 16.5. *S. decaryi*, PVB 5960, near Fort Dauphin, Madagascar, very large clump on exposed granite slope, in habitat, December 1993.



Fig. 16.6. *S. decaryi*, PVB 6191, near Zazafotsy, Madagascar.

2. *Stapelianthus pilosus*

Stapelianthus pilosus Lavranos & D.S. Hardy,
J. S. African Bot. 27: 237 (1961).

Trichocaulon decaryi Choux, *Ann. Inst. Bot.-Geol.*

Colon. Marseille Ser. 4, 10: 10 (1932).

Lectotype: Madagascar, Mount Angavo, 1 April 1931, R. Decary 8820 (P, holo.; K, TAN, iso.).

Stems 30-300 mm long, 8-12 mm thick, decumbent (rarely procumbent), green (purplish when exposed), smooth, covered densely with conical tubercles each tipped with a filiform leaf-rudiment 2.5-6.0 mm long, leaf-rudiment rapidly drying out to a persistent recurved whitish hair. **Pedice** 3-7 mm long, 1.0-1.5 mm thick, ascending, holding flower facing at least partly upwards, green sometimes speckled with purple and sometimes with scattered papillae towards apex; **sepals** 3.0-4.5 mm long, 1.0-1.5 (-2.0) mm broad at base, subulate, acuminate-filiform usually curling backwards towards apex, green sometimes speckled with purple, smooth. **Corolla** 10-18 mm diam., campanulate; outside cream spotted with maroon; inside covered with slender columnar papillae 0.50-0.75 mm long each with a sharp apical bristle, cream to pale yellow spotted with dark purple; **tube** 3-4 mm long, cupular, sometimes slightly thickened towards mouth; **lobes** 3.5-7.0 mm long, 4-6 (-9) mm broad at base, deltate, usually spreading with apices somewhat recurved. **Corona** 3.5-4.0 mm tall, 2.5-3.0 mm broad, dark maroon, seated on short stipe; **outer lobes** 2.4-3.5 mm long, fused for nearly half length of gynostegium, erect with spreading apices, convex outside and somewhat concave within, deeply bifid into narrowly $\pm$ parallel narrowly lanceolate acute lobules; **inner lobes** $\pm$ 0.4 mm long, deltoid, obtuse, usually not exceeding anthers.

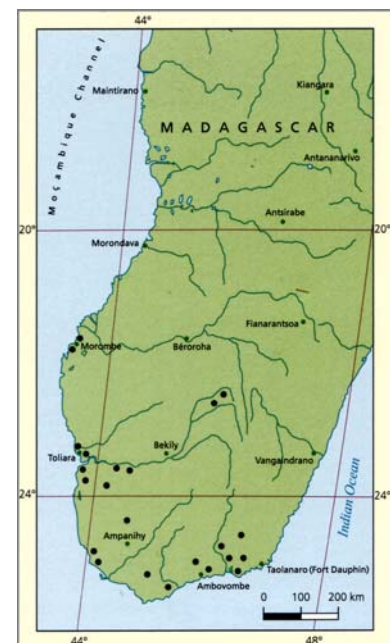


Fig. 16.7. Distribution of *Stapelianthus pilosus*.

Distribution and habitat

Stapelianthus pilosus is only known in the southern portion of Madagascar between Behara in the east and the mouth of the Onilahy River near Tulear in the west. It is not uncommon, for example, around Tsihombe, but few records have been made.

Occasionally *S. pilosus* will be found growing among small bushes in denuded areas, but it appears to prefer xerophytic, didiereaceous forests, where it flourishes in accumulations of leaf-litter in fairly shady spots on the forest floor. It has also very occasionally been recorded growing on exposed rocks.

Diagnostic features and relationships

When exposed, the stems of *S. pilosus* are comparatively short and erect, but when sheltered, they are prostrate and may reach 300 mm long. The plants tend to form mats of very variable



Fig. 16.8. *S. pilosus*, PVB 5959, Tsihombe, Madagascar, in habitat, December 1993.

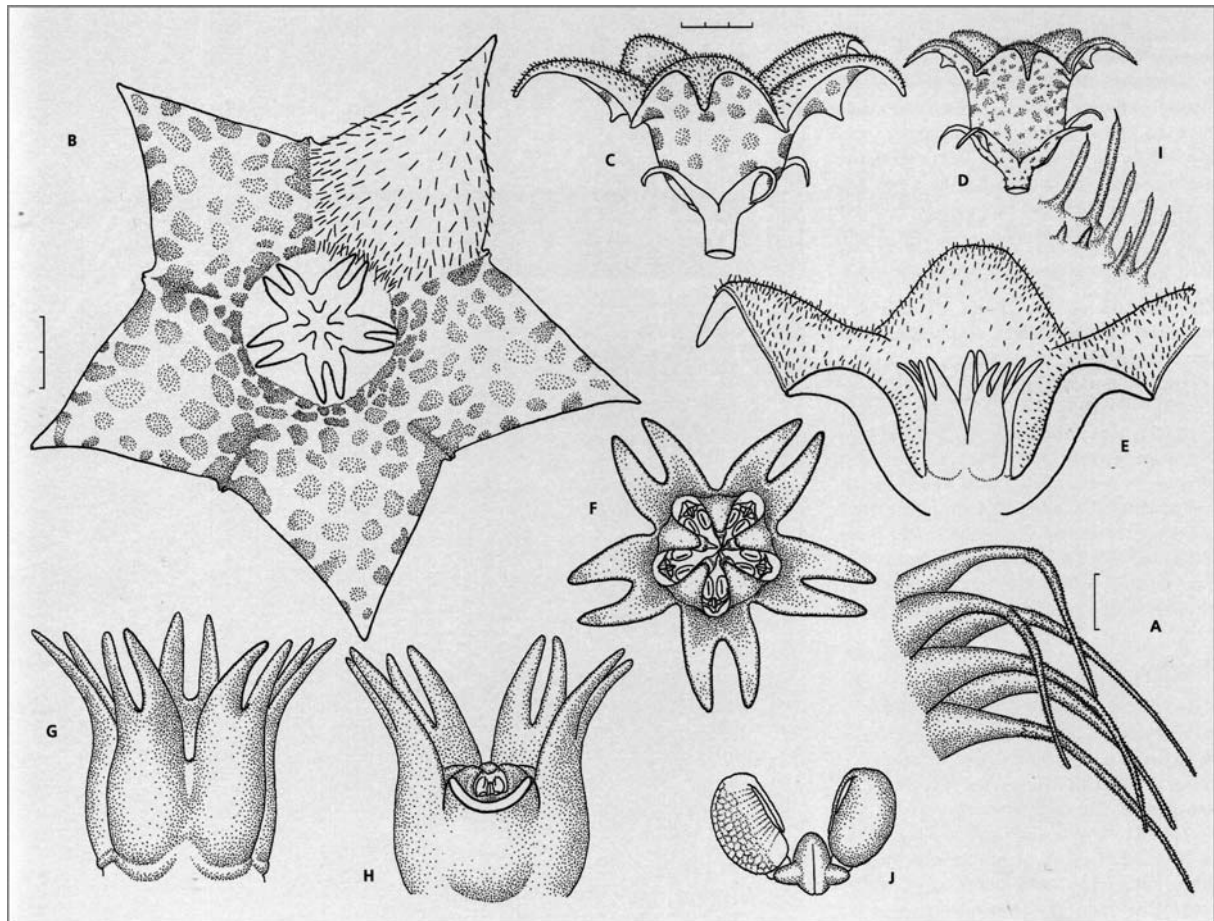


Fig. 16.9. *Stapelianthus pilosus*. A, tubercles on stem. B, face view of flower. C, D, side view of flower. E, side view of dissected flower. F, face view of gynoecium. G, side view of gynoecium. H, side view of gynoecium with one outer corona lobe removed. I, papillae inside corolla near base of lobes. J, pollinarium. Scale bars: A, 1 mm; B, E, 2 mm (at B); C, D, 3 mm (at C); F-H, 1 mm (at C); I, 0.5 mm (at C); J, 0.25 mm (at C). Drawn from A, D, I, J, PVB 5959, Tsihombe, Madagascar; rest, *hort. De Boer*.

STAPELIANTHUS PILOSUS

size, often dying off at one end and spreading by new growth at the other.

Choux described this remarkable plant as *Trichocaulon decaryi*, because of the cylindrical stems with many irregularly arranged, bristly tubercles. These uniformly coloured, smooth stems are very unusual indeed, being cylindrical and mostly creeping with an ascending to erect apex. They are densely covered with small, conical tubercles and these are arranged in spiralling rows near the tips of the stems but become disorganised lower down. Each tubercle tapers into a recurved, hair-like leaf-rudiment which rapidly dries out. The tubercles are close together so these dried-out, white husks of the leaf-rudiments afford the stems some protection, making the actual surface hard to reach.

These stems are unique in *Stapelianthus*. More normal for the genus, are the small groups of flowers that develop in gradual succession near the base of the stem. The sepals are rather longer and more slender than is usual, especially in relation to the size of the flower.

The flower in *S. pilosus* seems to be particularly variable in size and may be as little as 10 mm across. Outside it is smooth and spotted with dark purple on cream and inside there is a similar mottling with irregular spots on a slightly darker yellowish background. The inside is covered, densely on the lobes and mouth of the tube and more sparsely lower down, with slender papillae, each tipped with a fine bristle.

Inside the small, often relatively narrow tube, the dark maroon corona is seated on a very short stipe with erect, deeply bifid outer lobes. These lobes are fused into a cup more or less to the middle but apart from this the whole structure is typical of *Stapelianthus*. Unusual features are that there is remarkably little space between the guide-rail and the outer corona (compensated for by the small and narrow pollinia); the guide-rails are nearly erect rather than shallowly sloping; the anthers are horizontal; and the pollinarium is small, with small pollinia, with a disproportionately large corpuscle with small, round, lateral wings.

History

Material in the Paris herbarium indicates that Raymond Decary first discovered *S. pilosus* at Mount Kokomba (west of Beloha) in January 1918, so that this is the first species of *Stapelianthus* that he discovered.

This species was described as a *Trichocaulon* because of the unusual stems, with their almost cactus-like form. In 1959 it was recollected by Werner Rauh. This material led to its being transferred to *Stapelianthus*, as the inflorescences and flowers bore no resemblance to any in *Trichocaulon* but were similar to those

typical of *Stapelianthus*. Since the name *Stapelianthus decaryi* already existed, a new specific name had to be found for it and the epithet '*pilosus*' was chosen.



Fig. 16.10. *S. pilosus*, PVB 5959, Tsihombe, Madagascar.

3. *Stapelianthus arenarius*

Stapelianthus arenarius Bosser & Morat, *Adansonia* N.S. 11:340(1971).

Type: Madagascar, route to Manombo north of Tulear, Bosser & Morat 20392 (P).

Stapelianthus calcarophilus Morat, *Bull. Mus. Natl. Hist. Nat.*, B, *Adansonia*, 12: 3 (1990).

Type: Madagascar, Itampolo, Morat 3973 (P).

Stems 50-150 mm long, 5-10 mm thick, procumbent often with apices ascending, grey-green marked with purple-brown, surface bullate; **tubercles** arranged roughly into 4 rows, tipped with a small narrowly lanceolate recurved leaf-rudiment 1-2 mm long and 0.5 mm broad, slightly flattened above, gradually withering away. **Pedicels** 3-10 mm long, 1.0-1.5 mm thick, erect, holding flower facing upwards, pinkish green; **sepals** 2.0-4.0 mm long, 1.5 mm broad at base, lanceolate-acute, whitish. **Corolla** 20-25 mm diam., $\pm$ rotate; outside dull white finely dotted with pale maroon; inside finely papillate over whole surface except base (papillae up to 0.3 mm tall), white with few maroon spots becoming larger towards base and coalescing behind corona; **tube** $\pm$ 2 mm deep, very broad and shallowly bowl-shaped, containing gynostegium, not thickened around mouth; **lobes** 8-13 mm long, 4.5-5.5 mm broad at base, deltate, acute, spreading to recurved. **Corona** 2 mm tall, 4-5 mm broad, maroon-black, seated on very short stipe; **outer lobes** 2.5-2.8 mm tall, spreading, free practically to base, bifid to below level of inner lobes into slightly ascending-spreading narrowly obtuse teeth; **inner lobes** 0.7-1.0 mm long, linear oblong, $\pm$ adpressed to and equalling anthers.

Distribution and habitat

Very little is known about the distribution of *S. arenarius*. A few records have been made to the north of Tulear and it was found in a single spot near Itampolo (the type locality of *S. calcarophilus*), which lies well to the south of Tulear.

Stapelianthus arenarius was seen growing in fine, deep, red sand within 1 km of the sea in an open forest north of Tulear which was dominated by *Didierea madagascariensis*. Plants are common here among leaf-litter under bushes and trees. Their wrinkled surface lends them an extraordinary resemblance to dried twigs. When conditions are very dry the stems become prostrate and partly hidden among dried leaves and then they are practically invisible, but when rain has fallen they rise out of the leaf-litter and become much more visible. Near Itampolo, they were recorded from calcareous outcrops.

Diagnostic features and relationships

The stems of *S. arenarius* are much more rugulose than those of the other species. The tubercles are arranged in four rows and the stems are not at all clearly 4-angled. This becomes accentuated when they are in a dry state, when they are barely recognisable at all as the stems of a stapeliad.

This species has unusual flowers. Since they are only shallowly plate-like, they are the flattest flowers in *Stapelianthus*. The corolla lobes are white (sometimes faintly brownish) and the flower becomes spotted with maroon



Fig. 16.11. Distribution of *Stapelianthus arenarius*.

towards the centre. Most of the corolla is covered with small papillae which peter out around the corona.

In *S. arenarius* the outer corona is also very spread out so that it does not project much above the level of the corolla lobes. The outer lobes are more deeply bifid than in any of the

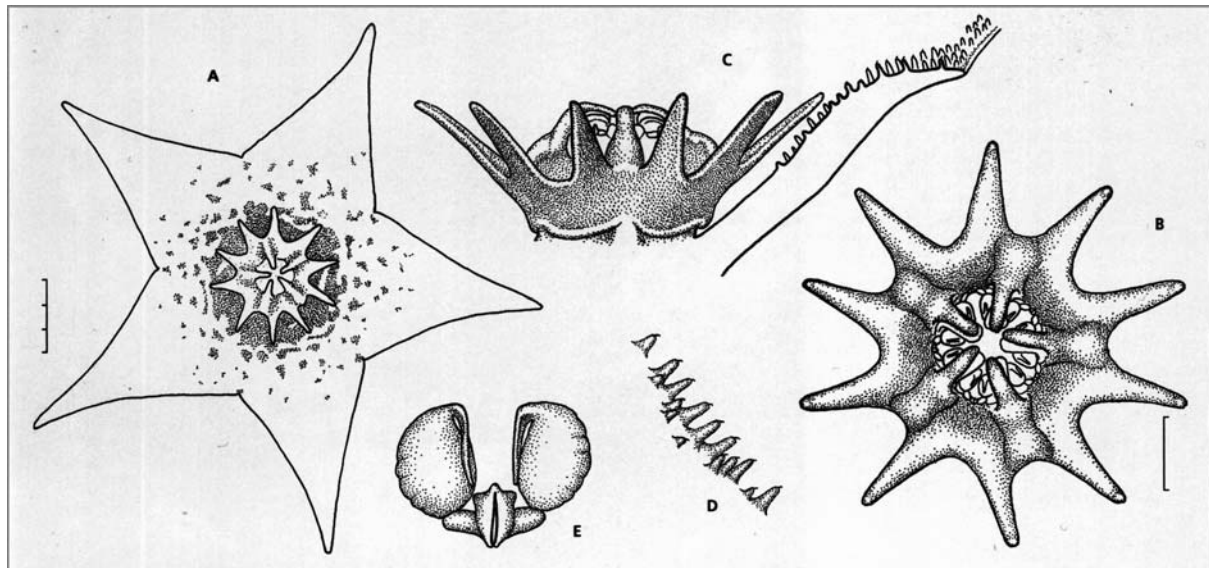


Fig. 16.12. *Stapelianthus arenarius*. A, face view of flower. B, face view of gynostegium. C, side view of gynostegium with part of corolla tube. D, papillae inside corolla near base of lobes. E, pollinarium. Scale bars: A, 3 mm; B, C, 1 mm (at B); D, 0.5 mm (at B); E, 0.25 mm (at B). Drawn from PVB 5954, north of Tulear, Madagascar.



Fig. 16.13. *S. arenarius*, PVB 5954, north of Tulear, Madagascar.

other species, with the division reaching right to the level of the bases of the inner lobes.

The rugose follicles are unique in the genus and among all the stapeliads.

Many features therefore make *S. arenarius* distinctive and it is not obviously related to any other species. The flowers are flatter than those of *S. madagascariensis* and have much shorter papillae on the inside. The corona is most similar to that of *S. madagascariensis*, but even this similarity is not close.

There seem to be no obvious reasons not to include *S. calcarophilus* under *S. arenarius*. In *S. calcarophilus* the sepals and flowers are smaller and the corolla lobes are reflexed. These minor differences seem to be outweighed by their being the same in all other features.

History

Stapelianthus arenarius was discovered by Jean Bosser and Philippe Morat in February 1970. The plants described as *S. calcarophilus* were discovered by Morat in April 1972.

4. *Stapelianthus keraudreniae*

Stapelianthus keraudreniae Bosser & Morat, *Adansonia* N.S. 11: 337 (1971).

Type: Madagascar, Betioky district, Ankazoabo gorge, Bosser & Morat 19413 (P).

Stems 25-150 (-400) mm long, 4-10 mm thick, forming dense to diffuse clumps, procumbent or with erect apices, purple-brown flecked on grey-green background, surface bullate; **tubercles** broadly flattened-conical, weakly joined into 4-5 (-7) angles along stem, tapering abruptly into small narrowly lanceolate recurved leaf-rudiment 1-2 mm long which is somewhat flattened above and gradually withers and falls off. **Pedicel** 3-7 mm long, 1.5 mm thick, ascending to erect, holding flower facing upwards; **sepals** 3-7 mm long, 1.5-2.0 mm broad at base, ovate-lanceolate, acute, green suffused faintly with purple. **Corolla**

20-35 mm diam., $\pm$ rotate; outside pale green finely spotted with red to brown (often arranged in 'veins'), with 3-5 raised longitudinal veins on each lobe, smooth; inside with scattered small obtusely conical usually purple-tipped papillae becoming longest (up to 0.3 mm long) and densest along edges of lobes and in mouth of tube but absent on outer side of annulus (sometimes only along margins of lobes), each tipped with small apical and often obtuse bristle, annulus somewhat shiny, pale red to dark purple-red or densely spotted with red-purple, lobes greenish to dull yellow spotted with wine- to purple-red; **tube** $\pm$ 3 mm long, 6-8 mm broad, pentagonal, broadening from base towards mouth, just containing gynostegium, thickened into cushion-like raised circular annulus around mouth; **lobes** 7-10 mm long, 8-12 mm broad at base, ascending to spreading or recurved, ovate, acute, usually with reflexed tips. **Corona** 3.0-4.5 mm tall, 5-6 mm broad, red to dark maroon, shiny, seated on very short stipe; **outer**



Fig. 16.14. *S. keraudreniae*, P.R. Alp, north of Betioky, Madagascar.

lobes 3.0-4.5 mm long, 2-3 mm broad, erect, spreading above close to mouth of tube, slightly concave outside and convex within, bifid in upper quarter to third into obtuse spreading to reflexed lobules; **inner lobes** ± 0.6 mm long, shorter than anthers, oblong-linear.

Distribution and habitat

Stapelianthus keraudreniae seems to occur only west and east of Betioky in the south-western corner of Madagascar.

In this area it has been recorded on sandstone hillsides (P.R. Alp, pers. comm. 1994; Rauh 1998).

Diagnostic features and relationships

The flowers of *S. keraudreniae* are more or less flat. In the centre there is a short tube that contains the corona. Around its mouth the corolla is slightly thickened and somewhat bent backwards, forming a conspicuous annulus. Beyond this the lobes spread out or are slightly recurved. Inside, the flower is finely spotted on the lobes and usually deeply coloured on the annulus, where it is also quite shiny. As usual there is considerable variation in colour, particularly from dark to quite pale red

and the annulus may be spotted or uniformly red. The flower emits a faint odour of excrement and some drops of a nectar-like secretion are sometimes found on the annulus. The papillae that are usually found on the flowers of *Stapelianthus* are present here too. The largest ones, which are very small compared to those in *S. madagascariensis*, are found along the margins of the lobes. On the face of the corolla they are even smaller and are very scattered.

The corona has the usual shape of the genus. The outer lobes are particularly short and tend to spread around the mouth of the tube towards the surface of the corolla. They are only slightly notched at their apices.

In their shape, the flowers of *S. keraudreniae* are reminiscent of those of, say, *Huernia zebrina*, except for being very much smaller. They are certainly very different from any other in *Stapelianthus*.

History

Stapelianthus keraudreniae was discovered by Jean Bosser and Philippe Morat in February 1964. Morat made several collections of this species north-east of Betioky but only recorded it once to the west of the town at the type locality.



Fig. 16.15. Distribution of *Stapelianthus keraudreniae*.

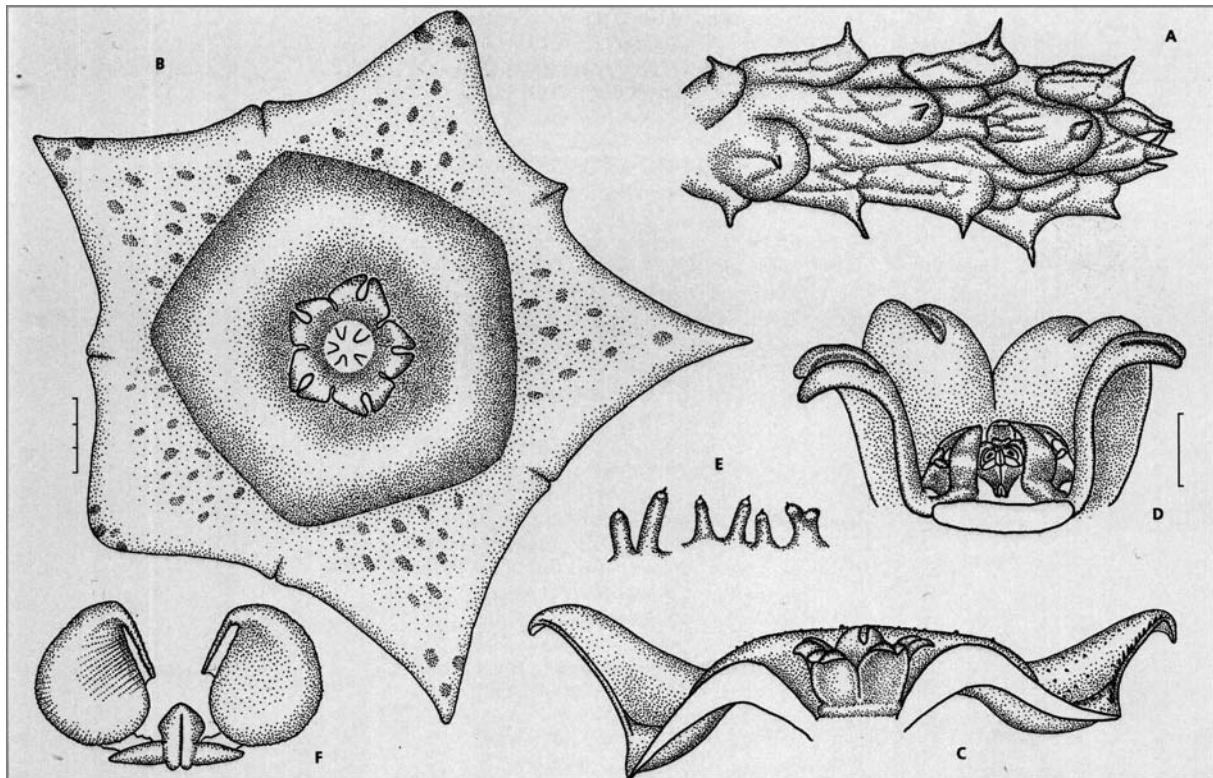


Fig. 16.16. *Stapelianthus keraudreniae*. A, portion of stem. B, face view of flower. C, side view of dissected flower. D, side view of gynostegium with one outer corona lobe removed. E, papillae inside corolla along edges of lobes. F, pollinarium. Scale bars: A-C, 3 mm (at B); D, 1 mm; E, 0.5 mm (at D); F, 0.25 mm (at D). Drawn from hort. J.H. van der Merwe.

STAPELIANTHUS INSIGNIS



Fig. 16.17. *S. insignis*, PVB 5953, east of Tulear, Madagascar.

5. *Stapelianthus insignis*

Stapelianthus insignis Desc., *Naturaliste Malgache* 9:181-182 (1957).

Type: Madagascar, 21-23 km from Tulear towards Tongobory near the Onilahy River, *Descoings* 2751 (TAN, missing).

Lectotype: *Naturaliste Malgache* 9: fig. 1 a-f.

Stapelianthus insignis subsp. *tongoboryensis* Rauh, *Trop. Subtrop. Pflanzenwelt* 85: 36 (1993).

Type: deciduous forests near Tongobory, *Rauh* 21874 (HEID).

Stems 50-200 mm long, 5-12 mm thick, procumbent to decumbent, often with apices ascending, (red- to) grey- to cream-green marked with purple-brown, surface bullate; **tubercles** broad and flattened, somewhat joined into 4 (-5) rows along stem so that stem $\pm$ square in cross-section, tapering abruptly into small narrowly lanceolate spreading to recurved leaf-rudiment 1-2 mm long which

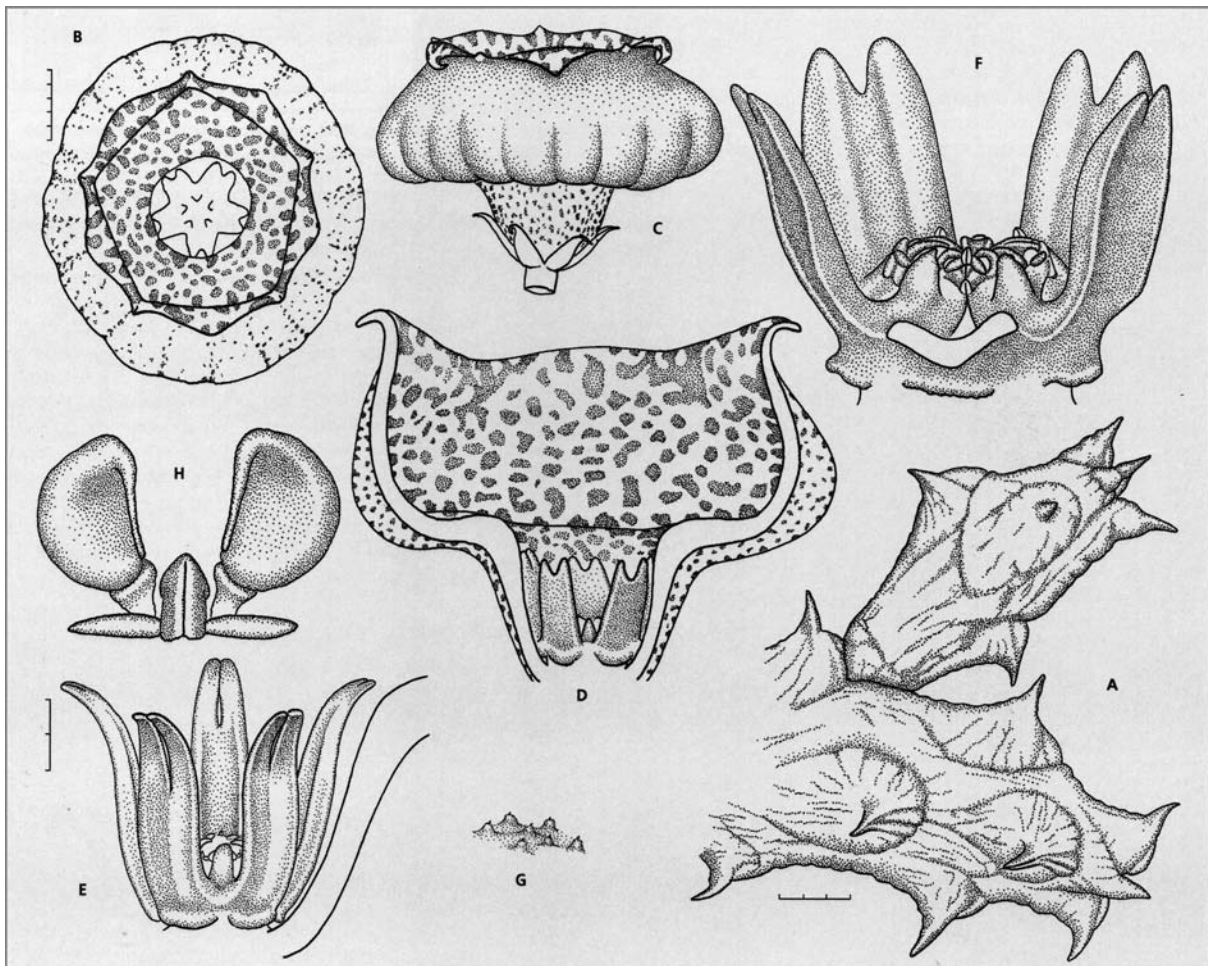


Fig. 16.18. *Stapelianthus insignis*. A, portion of stem. B, face view of flower. C, side view of flower. D, side view of dissected flower. E, side view of gynostegium. F, side view of gynostegium with one outer corona lobe removed. G, papillae inside corolla along edges of lobes. H, pollinarium. Scale bars: A, D, 3 mm (at A); B, C, 5 mm (at B); E, 2 mm; F, 1 mm (at E); G, 0.5 mm (at E); H, 0.25 mm (at E). Drawn from A, E, G, H, PVB 6208, south-east of Tulear, Madagascar; rest, *hort. De Boer*.

is slightly flattened above, gradually withering and falling off. **Pedice**l 4-8 mm long, 1-2 mm thick, ascending-erect and holding flower facing $\pm$ upwards, sometimes longitudinally grooved, purplish; **sepals** 5-8 mm long, 2-3 mm broad at base, subulate with narrow slightly recurved apex, smooth. **Corolla** 17-26 mm diam. at max., bicampanulate; outside pale green finely to boldly speckled with purple; inside smooth except for few small papillae along edge of corolla lobes, boldly speckled with purple on pale yellow-green; **tube** 5-10 mm long, 6-7 mm broad, cupular, fabric noticeably thickened at mouth beyond which corolla widens to maximum and then constricts to sometimes very narrow pentagonal mouth (6-16 mm diam.); **lobes** $\pm$ 2-3 mm long, 3-10 mm broad at base, broadly and very shortly triangular, acute, usually recurved. **Corona** 4.5-6.0 mm tall, 4-6 mm broad, dark maroon, seated on short stipe; **outer lobes** 4.0-7.5 mm long, free practically to base, erect to slightly spreading, concave outside and with slight medial groove inside, deeply to only shallowly bifid into $\pm$ parallel lobules; **inner lobes** $\pm$ 0.6 mm long, deltoid, obtuse, not usually exceeding anthers.

Distribution and habitat

Stapelianthus insignis is a widely distributed species, occurring from the hills just east of Tulear (and possibly further north as well) southwards to Ejeda and Ampanihy (Rauh 1993: 36).

S. insignis mostly grows among pieces of limestone and small bushes (very often a small, spiky gregarious member of the Asteraceae). Plants are mainly found along the edges of denser bush on calcareous flats or on the lower slopes of whitish, calcareous hills.



Fig. 16.20. Distribution of *Stapelianthus insignis*.



Fig. 16.19. *S. insignis*, PVB 5957, Ejeda, Madagascar.

Diagnostic features and relationships

The stems of *S. insignis* are difficult to separate from those of *S. madagascariensis* or *S. keraudreniae*, although they are generally a bit more square in cross-section than the others usually are.

The flowers of this species have a particularly unusual shape. There is a narrow 'primary tube' which closely surrounds the corona and which has a somewhat thickened mouth. Beyond this, the corolla forms a second bell-shaped part with the small lobes spreading at its mouth. This curious shape is somewhat similar to that in *Huernia erectiloba*. In both of these species the buds remain more or less cylindrical until they are about 8 mm long, after which the upper part begins to swell outwards somewhat below the bases of the corolla lobes. This outward swelling ultimately gives the corolla its bicampanulate shape and produces a bud with a roughly flat upper surface with the folds at the sinuses of the lobes projecting from this surface quite close to its centre and pointing in the direction of the centre. So, during this development, the lobes remain quite short. This causes the expansion of the lower part of the corolla to outpace that of the lobes and leave them behind near the centre of the bud.

The flowers seem to be extremely variable in colour and also in the degree to which the mouth of the tube is constricted. Descoings' original material was practically plain pale green outside with a very narrow mouth to the flower ($\pm$ 6 mm diam.). Some subsequent collections from the same area have had a boldly spotted corolla (outside) with much broader opening (up to 16 mm diameter) and some of these were described as a new subspecies by Rauh. However, this variation seems to be typical of

populations in this area and there is no reason to believe that two geographically discrete colour forms are involved. It would be more reasonable to consider them all as variants of a single species and consequently this subspecies is not recognised.

No odour has ever been noticed on the flowers of *S. insignis*.

History

Stapelianthus insignis was discovered by Pierre-Rene Montagnac near Tongobory and he showed it to Bernard Descoings in 1957.



Fig. 16.21. *S. insignis*, PVB 6208, south-east of Tulear, Madagascar.

STAPELIANTHUS MONTAGNACII

6. *Stapelianthus montagnacii*

Stapelianthus montagnacii (Boiteau) Boiteau & Jean Bertrand, *Cactus (Paris)* 26:116 (1950).
Stapelia montagnacii Boiteau, *Bull. Trimestriel Acad. Malgache* N.S. 24: 83 (1942).

Type: Madagascar, near Tulear, fl. Dec. 1941, *Montagnac sub Jardin Bot. Tananarive* 4938 (TAN, missing).

Lectotype: *Cactus (Paris)* 26:116, photo by G. Richard (1950).

Stapelianthus hardyi Lavranos, *Natl. Cact. Succ. J.* 26:67(1971).

Type: Madagascar, near Morombe, *Hardy & Jacobsen* 3569 (P, holo.; FT, K, PRE, iso.).



Fig. 16.22. *S. montagnacii*, PVB 6203, $\pm$ 50 km south of Morombe.

Stems 25-300 mm long, 6-10 (-15) mm thick, procumbent often with ascending apices, mottled with green to purplish on grey to cream background, surface bullate; **tubercles** broad and flattened to conical, weakly joined into 4 (-6) angles along stem, tapering abruptly into small narrowly lanceolate recurved leaf-rudiment 1-2 mm long, grooved above leaf-rudiment, leaf-rudiment slightly flattened above and gradually withering and falling off. **Pedice** 7-12 mm long, 2.0-2.5 mm thick, spreading and holding flower facing horizontally; **sepals** 2.5-3.0 mm long, 1.5 mm broad at base, ovate-triangular, acute, smooth, with recurved apices. **Corolla** (13-) 20-30 mm diam., shallowly campanulate; outside maroon becoming cream with maroon to red spots towards apex of lobes and base; inside densely covered (in maroon portion except at tips of lobes) with slender cylindrical maroon papillae up to 3 mm long usually slightly thickened towards apex and with spherical apical 'bristle', maroon to red on lobes and onto mouth of tube, below this cream concentrically speckled with maroon to red becoming plain cream in base of tube; **tube** 4-10 mm long, 9-17 mm broad, shallowly to deeply bowl-shaped, sometimes somewhat thickened around mouth; **lobes** 6-9 mm long, 6-9 mm broad at base, deltate, acute to acuminate, erect to spreading. **Corona** 4-6 mm tall, 6-8 mm broad, dark red, seated on short stipe; **outer lobes** 4-5 mm long, free practically to base, erect, concave outside and convex inside with groove down middle, rather variably bifid in upper third into erect deltoid lobules often with a smaller third one between them; **inner lobes** $\pm$ 0.5 mm long, $\pm$ deltoid, much shorter than to equalling anthers.



Fig. 16.23. Distribution of *Stapelianthus montagnacii*.

Distribution and habitat

Stapelianthus montagnacii is known from the area around Tongobory, south-east of Tulear. Material that may be ascribed to this species has also been collected north of Tulear. The plants traditionally known as *S. hardyi* occur from Morombe southwards for at least 50 km along the coast. The type locality, near Morombe on the west coast of Madagascar, is by far the northernmost record for any *Stapelianthus* it might also occur north of Morombe since the forest dominated by *Didierea madagascariensis*,

with which it is associated, extends northwards to just south of Morondava (Rauh 1978:11).

Stapelianthus montagnacii has been seen on sand among trees of *Didierea madagascariensis* and among thick leaf-litter on the floor of thickets of *Euphorbia tirucalli* and *E. intisy* growing on loam. Specimens were also found on limestone outcrops where they were wedged into crevices or between stones and small bushes.

In several of the spots where it was seen in December 1994 near Morombe and north

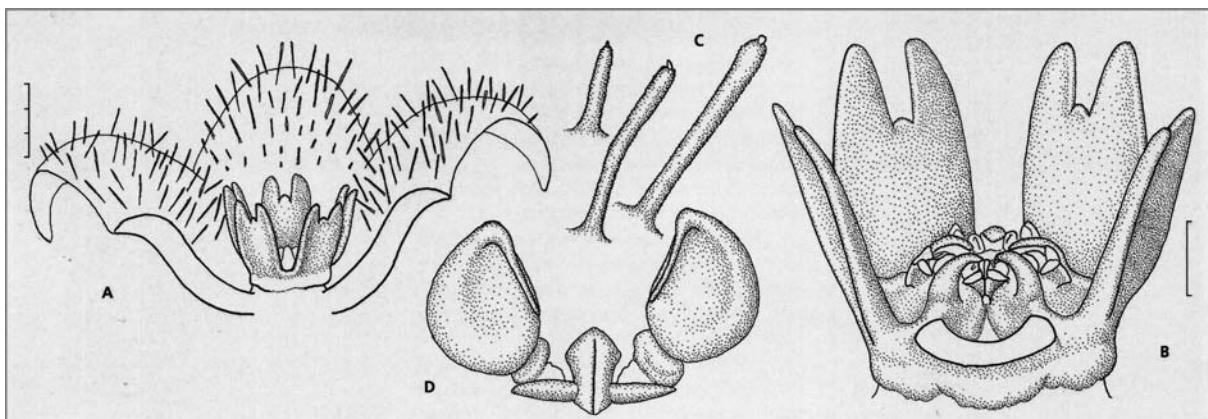


Fig. 16.24. *Stapelianthus montagnacii*. A, side view of dissected flower. B, side view of gynoecium with one outer corona lobe removed. C, papillae inside corolla near base of lobes. D, pollinarium. Scale bars: A, 3 mm; B, 1 mm; C, 0.5 mm (at B); D, 0.25 mm (at B). Drawn from *hort. De Boer*.

of Tulear, the species was found to be quite unbelievably common, forming a virtual groundcover on limestone rocks just above the level of the adjoining tidal mangrove thickets (south of Morombe) and on the floor of *Euphorbia* thickets. On limestone outcrops south of Morombe it was often associated with the recently described *Cynanchum hardyi*.

Diagnostic features and relationships

Plants of *S. montagnacii* often develop into enormous clumps. These were frequently seen to cover well in excess of 2 m in diameter and these large plants sometimes overflowed into the nearby road. The stems are mainly prostrate with an upturned apex, becoming more erect when more exposed. Their surface is dark and somewhat rugulose.

Stapelianthus montagnacii often has relatively large flowers, with a deep, bowl-shaped tube which may reach 8-10 mm long and lobes which spread out at its mouth. The whole of the corolla is usually about 2 mm thick and fairly rigid. The outside of the corolla is darkly coloured with a few spots on the lobes. Inside it is similarly dark, mainly maroon, and only



Fig. 16.25. *S. montagnacii*, PVB 6195, $\pm$ 30 km north of Tulear, Madagascar, in habitat, December 1993.

in the base around the corona is this colour relieved, becoming cream with maroon spots. Cylindrical hairs are plentiful inside, usually forming a dense carpet on the lobes (except near their tips) and to about the middle of the

tube, where they abruptly disappear at the end of the solid red area inside the mouth of the tube. The flower emits an odour of excrement.

There seems to have been some uncertainty expressed in the literature about

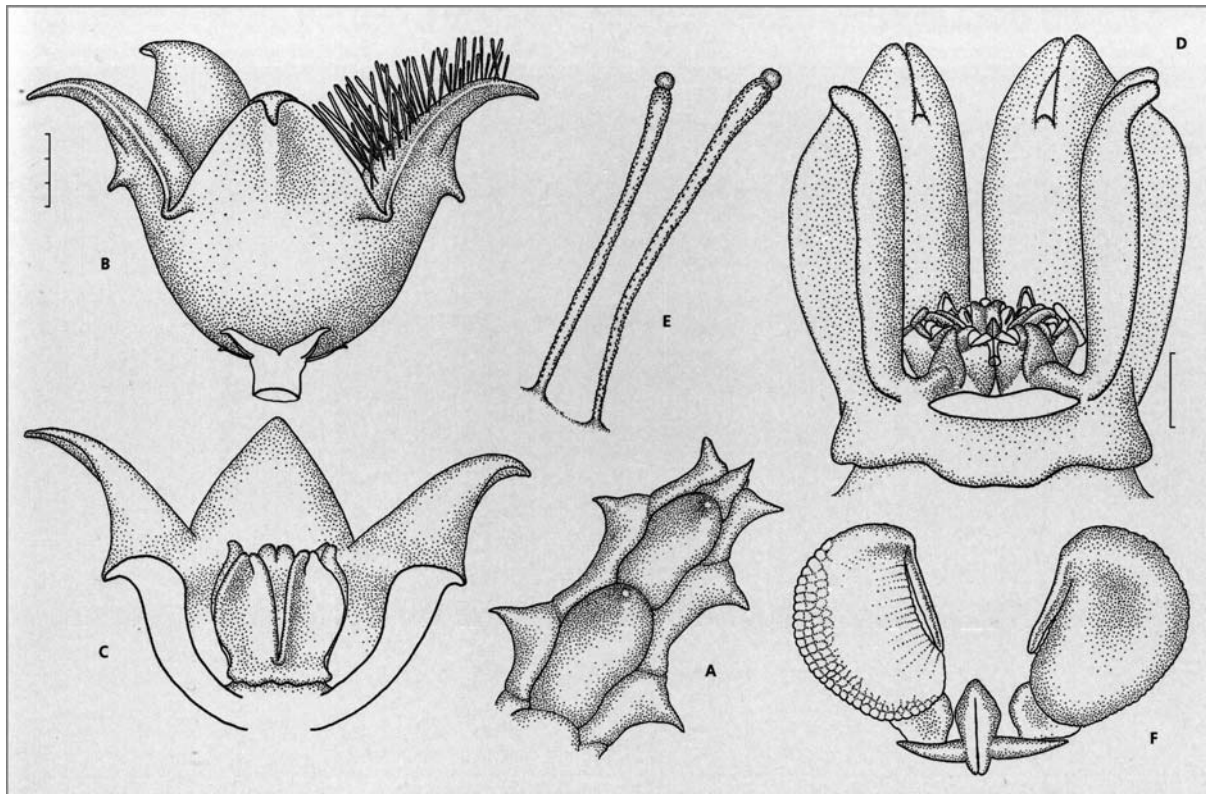


Fig. 16.26. *Stapelianthus montagnacii* (material formerly referred to as *S. hardyi*). A, portion of stem. B, side view of flower. C, side view of dissected flower. D, side view of gynostegium with one outer corona lobe removed. E, papillae inside corolla near base of lobes. F, pollinarium. Scale bars: A-C, 3 mm (at B); D, 1 mm; E, 0.5 mm (at D); F, 0.25 mm (at D). Drawn from PVB 6200, Morombe, Madagascar.

STAPELIANTHUS MONTAGNACII

the distinctness of *S. madagascariensis* and *S. montagnacii* as species. Rauh (1963:148] listed all the differences that he could find between them. These amounted to the slightly thicker stems in *S. montagnacii*, the slightly longer corolla lobes in *S. montagnacii* (the lobes measured 7-8 mm long and 7 mm broad in *S. madagascariensis*, 6 mm long and 6 mm broad in *S. montagnacii*), the darker-coloured corolla in *S. montagnacii* (cream with small darker spots in *S. madagascariensis*) and the outer corona lobes that are only bifid in the upper third in *S. montagnacii* (divided to the middle in *S. madagascariensis*). He concluded that only one species was probably involved. Rauh (1963: 148) also mentioned that *S. montagnacii* is more difficult to cultivate than *S. madagascariensis* but this is a characteristic that is difficult to interpret taxonomically and may be related to the different edaphic conditions from which the plants originated. Of the differences, the most reliable appear to be the generally darker flower in *S. montagnacii* and the manner in which the outer corona lobes are far more deeply bifid in *S. madagascariensis*.

Later, Rauh also suggested that *S. hardyi* cannot be clearly separated from *S. madagascariensis* (Rauh 1998). However, the real problem with *S. hardyi* is that it is not possible to separate it from *S. montagnacii*.



Fig. 16.27. *S. montagnacii*, PVB 6195, $\pm$ 30 km north of Tulear, Madagascar.



Fig. 16.28. *S. montagnacii*, PVB 6195, $\pm$ 30 km north of Tulear, Madagascar.

Stapelianthus hardyi shares with *S. Montagnacii* the slightly thicker stems, the darker colour of the corolla and the outer corona lobes that are only bifid in their upper third. The main differences between them lie in the somewhat darker, more deeply bowl-shaped flower of *S. hardyi*, its slightly thicker corolla, the longer papillae on the corolla with the spherical apical 'bristle', the rather more massive outer corona lobes and the larger pollinia. However, material gathered some 30 km north of Tulear is intermediate between the two in many respects. Here the flower is not quite so dark and inside the mottling of maroon on cream may continue right to the mouth of the tube, the tube is shallower (at only 4-6 mm deep), the papillae on the corolla have spherical to elongated apical

'bristles' and the pollinia are smaller. It would seem that the most suitable arrangement is to place *S. hardyi* and *S. montagnacii* together.

History

Stapelianthus montagnacii was discovered by Pierre-Rene Montagnac in 1940 near Tongobory, which lies to the south-east of Tulear. Montagnac (1906-88) was Chief of the provincial agricultural service in Tulear, working for 32 years in Madagascar on the cultivation of fruit in the country. He was passionately interested in the local flora and *Alluaudia montagnacii* is also named after him. The material named *S. hardyi* was discovered by D.S. Hardy and Jacobsen on 12 April 1971 just south of Morombe.

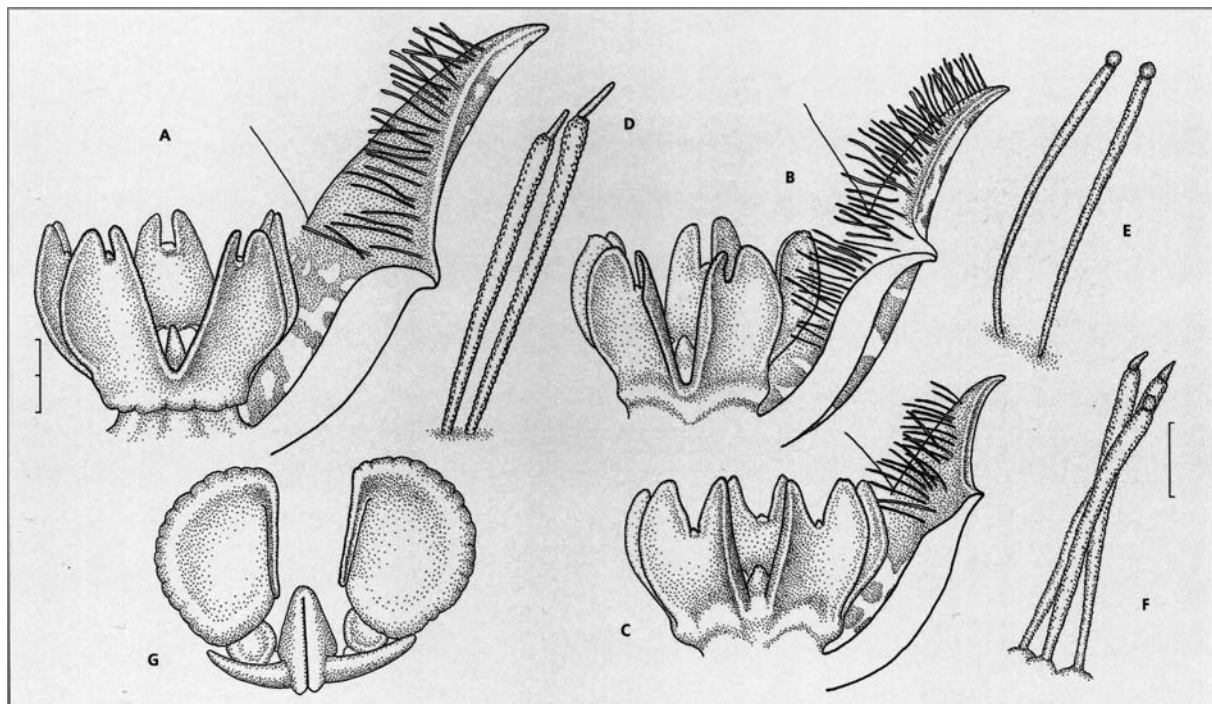


Fig. 16.29. *Stapelianthus montagnacii* (material intermediate between *S. montagnacii* and '*S. hardyi*')- A-C, side view of centre of dissected flower. D-F, papillae inside corolla along edges of lobes. G, pollinarium. Scale bars: A-C, 2 mm (at A); D-F, 0.5 mm (at F); G, 0.25 mm (at F). Drawn from A, D, G, PVB 6203, $\pm$ 50 km south of Morombe, Madagascar (similar to '*hardyi*' but corolla tube more mottled, outer corona lobes shorter and papillae with elongated apical bristle); B, C, E, F, PVB 6195, $\pm$ 30 km north of Tulear, Madagascar (mixed population with smaller flowers more like '*montagnacii*', papillae with variable apical bristle).

7. *Stapelianthus madagascariensis*

Stapelianthus madagascariensis (Choux) Choux in A.C. White & B. Sloane, Stap., ed. 1: 71 (1933).

Stapeliopsis madagascariensis Choux, Compt. Rend.

Hebd. Seances Acad. Sci. 193:1444 (1931).

Type: Madagascar, 15 km north of Ambovombe, Decary (P).

Stems 25-100 mm long, 3-9 mm thick, procumbent often with ascending apices, greyish marked with purple-brown, surface bullate; tubercles broad and flattened, very indistinctly joined into 4-6 angles along stem, tapering abruptly into small narrowly lanceolate recurved leaf-rudiment 1-2 mm long, which is slightly flattened above and gradually withers and falls off. **Pedicel** 3-6 mm long, 1.5 mm thick, spreading with erect apex holding flower facing upwards; **sepals** 3-5 mm long, 1-2 mm broad at base, ovate-lanceolate, acute, smooth. **Corolla** 20-28 mm diam., shallowly campanulate; outside pale green to cream spotted with maroon (spots becoming finer towards base and apices of lobes); inside cream spotted with maroon (fading away in tube), covered except in tube with long slender white cylindrical papillae up to 2 mm long with minute obtuse apical bristle; **tube** 4-7 mm long, 10-12 mm broad, shallowly bowl-shaped; **lobes** 6-9 mm long, 6-10 mm broad at base, broadly deltate, acute, spreading to recurved. **Corona** 3.5-1.0 mm tall, 4.5-6.0 mm broad, dark maroon, $\pm$ sessile; **outer lobes** $\pm$ 3 mm long, free practically to base, erect to slightly spreading, sometimes concave outside and slightly convex within, bifid at least to middle, with lobules narrowly deltoid and slightly diverging to obtuse and erect; **inner lobes** $\pm$ 0.6 mm long, narrowly deltoid to $\pm$ linear, sometimes exceeding anthers.

Distribution and habitat

Stapelianthus madagascariensis is widespread in the southern part of Madagascar, though it has been only very scantily recorded. Records show it to occur mainly in the southern lowlands from Ambovombe to near Itampolo, at altitudes of 50-200 m. Morat (1995) also mentioned its occurrence at an altitude of about 800 m in the valley of the Menarahaka River, south-east of Ihosy on the southern edge of the escarpment.

Plants may grow among small bushes in denuded areas. However, they seem to grow equally well in accumulations of leaf-litter on the floor of dry, xerophytic forest, with various members of the Didiereaceae.

Diagnostic features and relationships

The stems of *S. madagascariensis* are generally prostrate with upturned apices and are very indistinctly 4-6-angled. They form dense mats that may reach 0.5 m in diameter.

The flowers of *S. madagascariensis* are shallowly bowl-shaped. Inside they are bright cream with small maroon spots over most of the surface. In some plants the spots fade in intensity in the tube while in others they coalesce around the corona. Most of the inside (except towards the corona in the tube) is adorned with long, slender, hair-like papillae which are often white. Outside, the corolla is also spotted brightly with red but these spots



Fig. 16.30. Distribution of *Stapelianthus madagascariensis*.

do not correspond to those inside.

The outer corona lobes tend to be deeply bifid, usually for at least half their length.

Stapelianthus madagascariensis is most closely allied to *S. montagnacii*. The two species

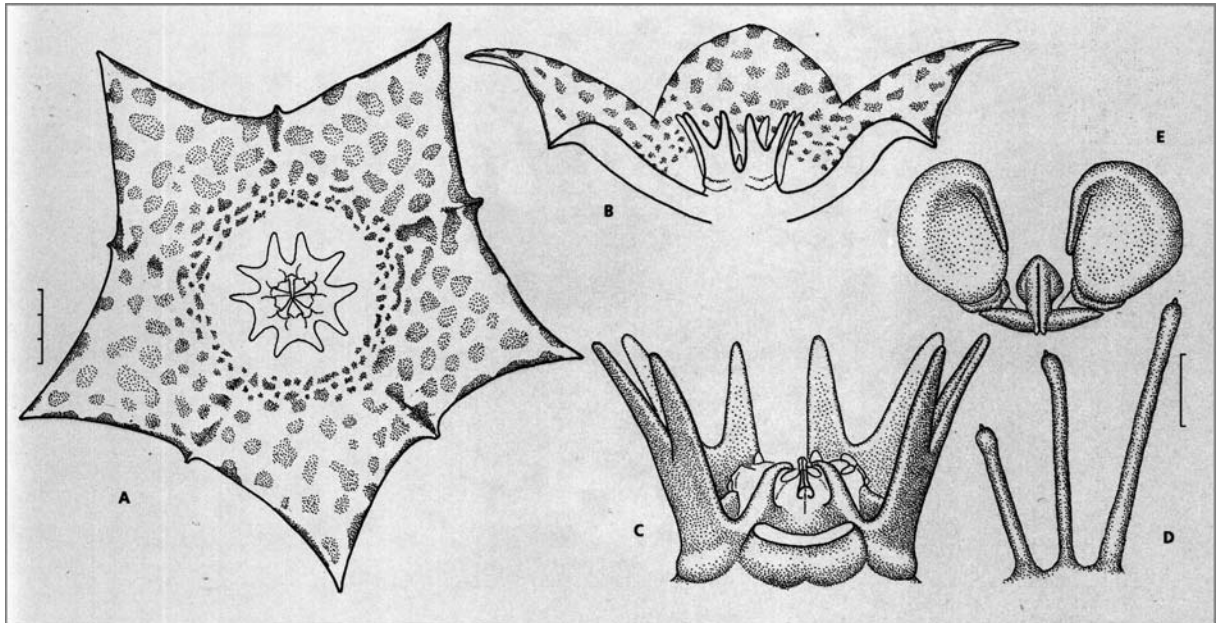


Fig. 16.31. *Stapelianthus madagascariensis*. A, face view of flower. B, side view of dissected flower. C, side view of gynostegium with one outer corona lobe removed. D, papillae inside corolla around mouth of corolla tube. E, pollinarium. Scale bars: A, B, 3 mm (at A); C, 1 mm (at D); D, 0.5 mm; E, 0.25 mm (at D). Drawn from PVB 5958, Tsihombe, Madagascar.

STAPELIANTHUS MADAGASCARIENSIS

seem to be reliably separable by the very indistinctly angled, often quite slender stems and the shallowly bowl-shaped flowers with small dark spots on a white background of *S. madagascariensis*. In *S. montagnacii* the stems are usually stouter and fairly clearly 4-angled and the flowers have a more deeply bowl-shaped tube. Inside, the flowers of *S. montagnacii* are darkly coloured and usually mottled with cream only near the base of the tube.

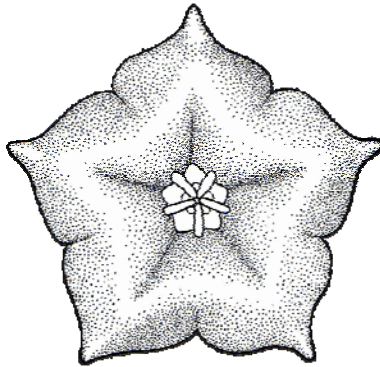
History

Stapelianthus madagascariensis was discovered by Raymond Decary in February 1931 about 15 km north of Ambovombe. It was the second species that he found.



Fig. 16.32. *S. madagascariensis*, PVB 5958, Tsihombe, Madagascar.

17. Stapeliopsis



In 1928 Neville S. Pillans described the monotypic genus *Stapeliopsis* to accommodate the remarkable new species, *S. neronis*, which he considered to be very different from all other stapeliads because of its singular outer corona. In 1966 a further species, *S. urniflora*, was described but this did not share the remarkable corona with *S. neronis*. It was placed in *Stapeliopsis* essentially because of some similarities in the stems and the somewhat urceolate corona. An investigation of the species of *Pectinaria* showed that some of these were most closely related to those in *Stapeliopsis* and it was found that *S. exasperata*, which was only described in 1978, shared several characters with *S. urniflora*. Consequently, *Stapeliopsis* was expanded to accommodate four species of *Pectinaria* (Bruyns 1981a). Further, more recent investigations have confirmed this view. They have shown that this concept of *Stapeliopsis* defines a monophyletic entity (Bruyns 1999e) if morphological characters alone are used. This treatment showed that the two sections upheld in Bruyns (1981a) were not supported. A further investigation, which combined both morphological and molecular data (Bruyns *et al.* 2005) has shown again that *Stapeliopsis* is monophyletic, with high statistical support. Our analyses show that the genus splits into a northern branch, which is statistically very strongly supported (containing *S. khamiesbergensis*, *S. neronis* and *S. urniflora*) and the remainder with a more southerly distribution. This southern branch is unsupported and in it *S. exasperata* is sister to the other species. Since the support for the southern branch is so low, the two sections of Bruyns (1981a) are abandoned here. None of this provides any support for splitting *Stapeliopsis* into three genera as Plowes (2003b) proposed and these proposals are rejected.

Stapeliopsis Pillans, *S. African Gard. & Country Life* 18: 32 (1928), *non* Choux (1931), *nec* E. Phillips (1932).

Type: *Stapeliopsis neronis* Pillans.

Stapeliopsis sect. *Cageliorona* Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 75 (1981).

Type: *Stapeliopsis saxatilis* (N.E.Br.) Bruyns.

Hermanschwartzia Plowes, *Excelsa* 20:11 (2003).

Type: *H. exasperata* (Bruyns) Plowes.

Neopectinaria Plowes, *Excelsa* 20:12 (2003).

Type: *N. saxatilis* (N.E.Br.) Plowes.

Dwarf to small spineless sometimes rhizomatous succulent, forming clump or mat to 300 mm diam. **Stems** 4-35 mm thick, prostrate to decumbent or erect, fleshy and firm to hard, glabrous to finely papillate-pubescent, glaucous green or brownish to blue-green mottled with purple; **tubercles** 1-5 mm long, mostly laterally flattened and joined into 4 angles along stem, tapering to small often hard yellowish tooth, rarely with stipular denticles and without any obvious leaf-rudiment. **Inflorescence** glabrous to minutely pubescent, 1 (-3) per stem arising near base, with 1-6 flowers developing in gradual succession on knobbly peduncle usually short but up to 25 mm long, with few lanceolate bracts < 1 mm long without lateral teeth; **pedicel** 2-10 mm long, elongating (with follicles) to 25 mm long; **sepals** 2-4 mm long, 1 mm broad at base, mostly lanceolate, acute to acuminate. **Corolla** 9-28 (-32) mm long, 5-25 mm broad, ellipsoidal, ovoid to cylindrical or campanulate, shallowly lobed; outside glabrous and shiny (finely papillate in *S. khamiesbergensis* and *S. neronis*); inside not rugulose, velvety, mostly densely to sparsely papillate especially towards mouth of tube, papillae each with a stiff apical bristle, these bristles usually becoming longer (up to 2 mm) towards base of corolla, rarely not papillate and with bristles only; **tube** 2-24 mm long, 3-15 mm broad, making up most of length of flower an often narrowing strongly towards mouth; **lobes** 2-16 mm long, 2-7 mm broad at base, usually considerably shorter than

tube, sometimes remaining joined at tips, margins eciliate. **Corona** 2.5-11.0 mm tall, 2-5 mm broad, consisting of 2 series of lobes arising on staminal tube and partly or wholly intergrown, raised on short obtusely pentagonal stipe above base of corolla tube, glabrous except on outside in *S. neronis*; **outer lobes** < 1 mm long, emarginate, forming shallow pockets between bases of inner lobes and joined laterally to them or 1-11 mm long and fused into cup from < half of length of inner lobes to exceeding inner lobes; **inner lobes** 2-6 mm long, adpressed to anthers only near base, erect then connivent towards apices, laterally flattened at least in lower half, usually with conspicuous rounded-deltoid dorsal process around middle. **Anthers** horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** ellipsoidal, longer than broad, insertion-crest exactly along outer edge, caudicle attached with small $\pm$ circular pad to base. **Follicles** erect, terete-fusiform, borne on considerably elongated pedicel, obclavate, slender, consisting of 2 horns diverging at 30-60°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

Despite the small size of this genus, there is a remarkable range of variation in certain characters across it.

The stems are mainly 4-angled but vary from decumbent with a very short, horizontal portion (*S. neronis*) to extensively rhizomatous (*S. breviloba*, *S. exasperata* and to a much smaller degree *S. urniflora*) or prostrate (*S. pillansii*, *S. saxatilis* and *S. stayneri*). The shape of the plant depends very much on the habit of the stems and may be a dense but small clump or a mat-like cluster. The stems are very variable in thickness across the genus, from 4 mm thick in *S. breviloba* to 35 mm thick in *S. neronis* but only in *S. saxatilis* is there much variation in thickness within the species and here this is found sometimes even on one stem.

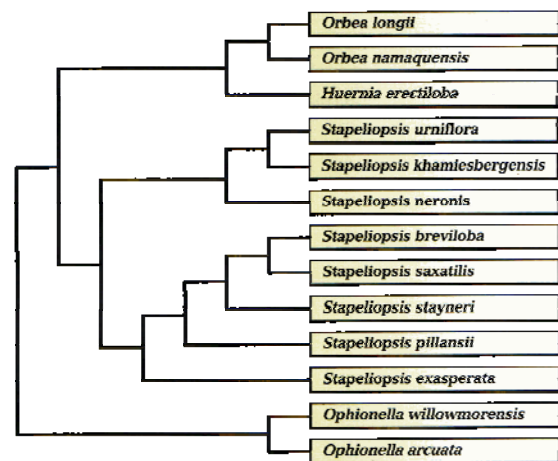


Fig. 17.1. Simplified cladogram derived from chloroplast, nuclear and morphological data, showing the possible relationships among the species of *Stapeliopsis* (Bruyns *et al.* 2005).

STAPELIOPSIS

In *S. neronis* and *S. urniflora* the stems are bluish green flecked with darker purple patches. In *S. saxatilis* they are mostly uniformly grey-green but are sometimes flecked with purple. In the remaining species they are always uniformly greyish or brownish green. Each tubercle on the stem is tipped with a conical leaf-rudiment which is not differentiated at all, but sometimes becomes quite hard and sharp in *S. saxatilis*.

There is quite remarkable variation in the cells of the epidermis of the stem where the outer walls vary from flat to extended into a prominent central papilla. These papillae are longest in *S. neronis* (fig. 18 D, E), where they are quite obvious; smaller in *S. khamiesbergensis* and *S. urniflora*, where they are not easily seen but can be felt; smaller again in *S. exasperata*, where the stem is smooth to the touch; smaller still to absent in *S. saxatilis*; and more or less absent in the others.

The inflorescences in *Stapeliopsis* mature near the base of the stem and there is usually

only one per stem. In *S. breviloba*, *S. exasperata*, *S. khamiesbergensis* and *S. urniflora*, where the stems may be rhizomatous and where the lower parts are therefore often well beneath the surface of the soil, the inflorescence frequently develops beneath the surface of the ground. The flowers may also end up being partly submerged, in some cases with just the lobes appearing above the surface. In *S. exasperata* this is the usual situation, with the corolla tube beneath the soil and the lobes spreading out on its surface. In *S. pillansii* the inflorescences on the lower surface of the stem develop (while those on the upper surface tend to remain inactive) and the flowers are pushed downwards into the soil. A small peduncle may develop in *S. neronis* and *S. pillansii* but generally the inflorescence becomes broader with increased activity rather than lengthening into a peduncle. The pedicel is usually slender and horizontal, bending upwards at its end to hold the flower erect in all species except *S. pillansii*. In *S. pillansii* the flower faces horizontally or

downwards. In all species the pedicel elongates markedly when the follicles begin to develop so that, even in the subterranean-flowered species, at maturity the base of the follicle is well above the surface of the soil.

The species of *Stapeliopsis* exhibit an unusually wide range in the shape of the flower, which may be anything from tubular or ellipsoidal to campanulate.

In *S. breviloba*, *S. neronis* and *S. urniflora* the corolla consists primarily of an ovoid or obovoid tube. This narrows gradually towards its mouth and so the overall shape is more or less ellipsoidal. In *S. exasperata*, *S. saxatilis* and *S. stayneri* the lobes are nearly as long as the tube; in *S. saxatilis* the tube is cupular to cylindrical or somewhat ovoid and the lobes are mostly joined at their tips, resulting once more in a more or less ovoid corolla; in *S. exasperata* the tube is cylindrical with the lobes usually spreading from the mouth. In *S. pillansii* the corolla is campanulate to pear-shaped with the broadly cupular tube only slightly longer than

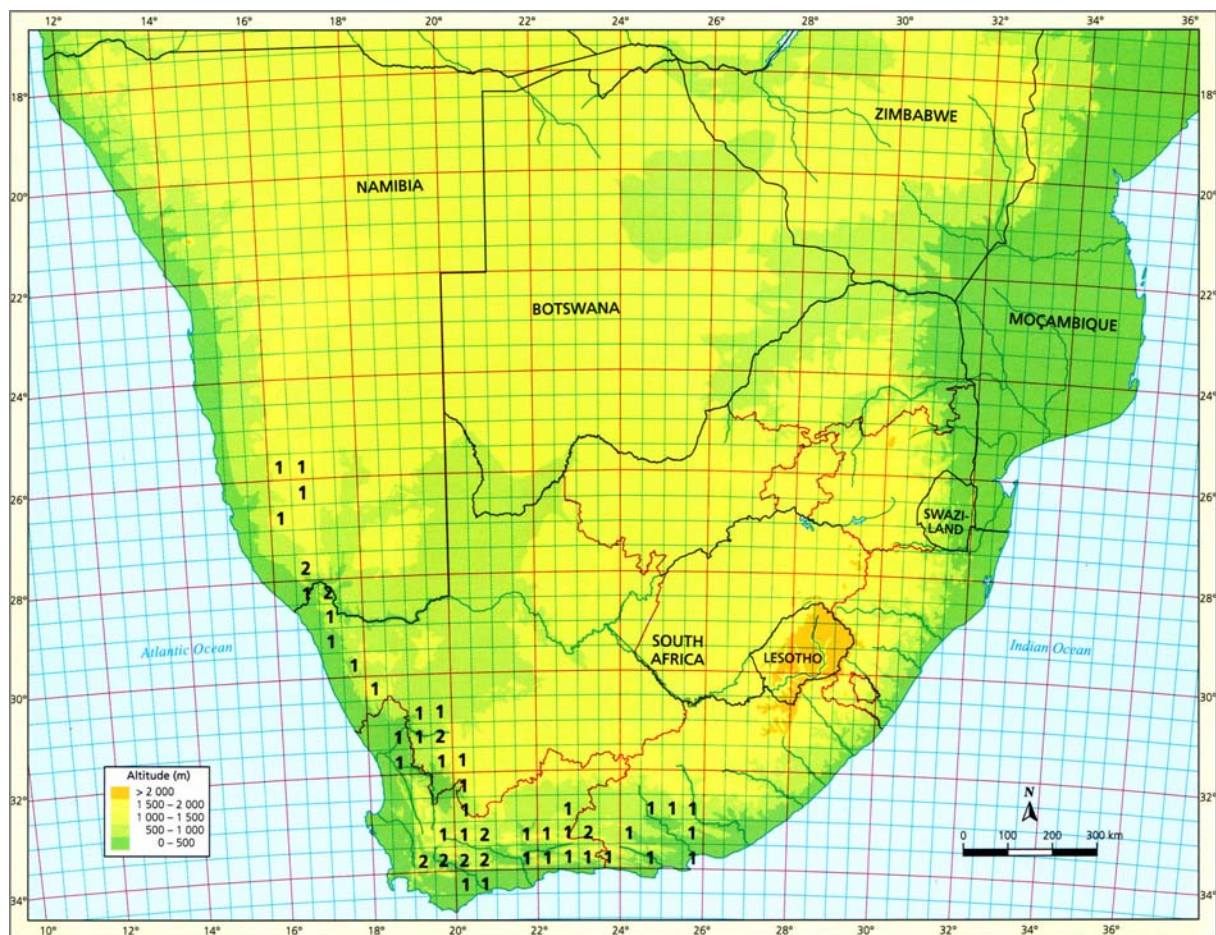


Fig. 17.2. Patterns of diversity in *Stapeliopsis*, showing the number of species recorded to date in each half-degree square.

Key to the species

1. Stems papillate, basal stipe of gynostegium broader than rest of gynostegium, outer corona lobes fused into tube so that anthers not visible from side 2.
2. Outside of corolla sparsely to densely papillate and dull, outer corona enclosing entire column 3.
3. Outside of corolla covered densely with sharp-pointed papillae, outer corona cylindrical with incurved flaps around its mouth **8. *S. neronis***
3. Outside of corolla sparsely and minutely papillate, outer corona conspicuously broadening towards mouth and vase-shaped, without incurved flaps around mouth **7. *S. khamiesbergensis***
2. Outside of corolla glabrous and shiny, outer corona tube enclosing lower half of column, lobes bifid into small outward-pointing teeth **6. *S. urniflora***
1. Stems smooth, basal stipe of gynostegium narrower than rest of gynostegium, outer corona lobe reduced to small tooth between inner lobes and anthers visible from side 4.
4. Plant rhizomatous and underground stems without angles, above-ground stems with erect tips 5.
5. Stems 8–15 mm thick, corolla inside with conspicuous somewhat cylindrical papillae, lobes 6–16 mm long **5. *S. exasperata***
5. Stems 4–7 (–9) mm thick, corolla inside ± devoid of papillae, lobes 2–3 mm long **1. *S. breviloba***
4. Plant not rhizomatous and all portions obviously 4-angled and similar in shape, stems horizontal 6.
6. Corolla thin, folds between lobes minute to absent, flowers above ground and produced facing upwards 7.
7. Corolla with bristles only in lower half of tube, outside pale pink to whitish near base **3. *S. stayneri***
7. Corolla with bristles over most of inside, outside wholly dark maroon to dark red **2. *S. saxatilis***
6. Corolla thick and rigid, folds between lobes almost half as broad as lobes, flowers usually subterranean and produced facing horizontally or downwards **4. *S. pillansii***

the lobes. *Stapeliopsis pillansii* is also unusual in that the corolla is exceptionally thick and rigid, which is presumably an adaptation to flowering underground, since a certain rigidity is essential for the flower to maintain its shape beneath the soil.

Inside the flower there are plenty of bristles and papillae. In *S. exasperata*, *S. neronis* and *S. urniflora* there are columnar papillae towards the mouth of the tube (with a few on the lobes too in *S. exasperata*), each of which is tipped with a short bristle. Towards the base of the tube the bristle becomes longer and the papillae on which each of them sits gradually disappears. In *S. breviloba*, *S. pillansii*, *S. saxatilis* and *S. stayneri* the papillae are more or less absent and only the apical bristles remain, being present over most of the lower half of the tube.

In all species the gynostegium is at least slightly raised above the base of the tube on a stipe. In *S. neronis* the stipe is slightly broader than the gynostegium at maturity (though narrower in earlier stages) whereas in *S. khamiesbergensis* and *S. urniflora* it is very much broader than the gynostegium and forms a platform on which the corona is seated. In the remaining species the bases of the outer corona lobes swell outwards and downwards to form a ring into which the stipe fits. In *S. khamiesbergensis* and *S. neronis* the corona appears to consist of a cylindrical tube. This remarkable structure is in fact the outer corona, which encloses the whole gynostegium. In *S. urniflora* much less of a tube is formed by the outer corona, which only rises up to the level of the tops of the anthers, and in the remaining species it is further reduced, exposing the anthers and the guide-rails. The odd form of the inner corona lobes, rising above the anthers

from near their base and laterally flattened, is the defining character for the genus. In species such as *S. saxatilis* the inner corona lobes have a prominent dorsal horn around their middle and raised ridges along their sides below this outgrowth. Ontogenetic investigations have shown that this horn and the ridges initially arise as a lateral extension of the outer lobes but are then all dragged upwards by strong growth of the tissue around the base of the inner lobes so that they appear to be dorsal outgrowths of the inner lobes (which is how they are referred to here in the descriptions).

The species of *Stapeliopsis* are found along the western side of southern Africa, mainly within and on the edges of the winter-rainfall zone of South Africa and Namibia. Records exist from the northern side of the Tiras Mountains south-west of Helmeringhausen, through Namaqualand and the western edge of Bushmanland (very few and scattered), above the escarpment between Calvinia and Sutherland to the western edge of the Great Karoo. There are many records from the Worcester-Robertson Karoo and the Little Karoo, but the species become rare once more from Willowmore eastwards to Somerset East.

Plants are usually well hidden, growing under bushes where leaf-litter collects. They are rarely common, except sometimes in the case of *S. saxatilis*.

Small flies have frequently been observed trapped within flowers of species such as *S. breviloba*, *S. neronis*, *S. saxatilis* and *S. urniflora*, fleeing their predicament when the flower is cut open for examination. I have never had the presence of mind to catch them to check for attached pollinia. Vogel (1954) examined

flowers of *S. neronis* and concluded that minute flies were involved in its pollination. The minuscule openings between the corolla lobes in *S. breviloba* and others, the very restricted mouth of the corolla tube in *S. neronis* and the frequent detection of tiny flies within the flowers makes it almost certain that these are the pollinators. It would appear that these flowers act as a trap in a very similar manner to flowers of many species of *Ceropegia*. The complex movements of the pedicel which are known to occur in *Ceropegia* to tip the flower over and release the trapped insects (Vogel 1961) have not developed here. In *S. exasperata* the flower may be submerged beneath loose leaf-litter, though the erect and cylindrical shape of the tube again suggests that it acts as a trap. A different syndrome appears to be involved in *S. pillansii*, where the campanulate flowers are mainly produced under the soil. This is also the only species where the flowers are not held erect. The underground flowering habit of *S. pillansii* is unique in the Apocynaceae.

STAPELIOPSIS BREVILOBA

1. *Stapeliopsis breviloba*

Stapeliopsis breviloba (R.A.Dyer) Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 81 (1981).

Pectinaria breviloba R.A.Dyer, *J. S. African Bot.* 20: 155 (1954).

Neopectinaria breviloba (R.A.Dyer) Plowes, *Excelsa* 20: 12 (2003).

Type: South Africa, Cape, Tweefontein near Worcester, fl. 1952, *Van Breda 183* (PRE, holo.; K, iso.).

Dwarf rhizomatous succulent forming clump 30-80 (-150) mm diam. **Stems** 10-60 mm long, 4-7 (-9) mm thick, decumbent with horizontal portion sometimes spreading up to 150 mm or more underground, above-ground portions erect, glabrous, grey-brown, smooth; **tubercles** 1-2 mm long, conical, joined near base into 4 obtuse angles along stem, tapering to fine acute spreading tooth. **Inflorescence** glabrous, usually developing near base of stem at level of soil or below from small often subterranean peduncle; **pedicel** 3-7 mm long, < 1 mm thick, spreading with ascending apex holding flower facing upwards; **sepals** $\pm$ 2.5 mm long, lanceolate, acute. **Corolla** 10-13 mm long, 5.0-6.5 mm diam., ellipsoidal (broadest near middle); outside glabrous, smooth, somewhat shiny pinkish brown to reddish towards base; inside pale flesh-coloured around mouth of tube and lobes, below this merging into deep maroon-black, velvety-smooth, with bristles up to 1 mm long in lower half of tube, some arising from low rounded papillae; **tube** 8-10 mm long, narrowing towards mouth; **lobes** 2-3 mm long, 2.0-2.5 mm broad at base, inflexed over mouth of tube, ascending towards and fused at tips, narrowly deltate, acute. **Corona** $\pm$ 3 mm tall, 2.5 mm broad, raised on white obtusely pentagonal stipe 0.5-1.0 mm long, deep maroon; **outer lobes** $\pm$ 0.5 mm long, ascending, truncate to finely denticulate, entire to emarginate, forming shallow pouch between bases of

inner lobes and fused laterally to them for entire length; **inner lobes** 2.0-2.4 mm long, erect then connivent at apices, laterally flattened becoming dorsiventrally flattened near obtuse slightly swollen tips, with obtuse and obscure spreading hump-like dorsal wing near middle.

Distribution and habitat

Stapeliopsis breviloba is found between Worcester and Swellendam and is most plentiful between Worcester and Robertson, especially on the south bank of the Breede River. Although it was always thought to be endemic to the Worcester-Robertson Karoo, it is also known from a single collection from west of Swellendam. However, many of the localities at which it was formerly known to grow have been destroyed by the burgeoning viticulture that is taking over much of this valley.

Plants are found under small bushes (often *Pteronia paniculata*) on low, stony ridges or in loam in flats.

Diagnostic features and relationships

The stems of *S. breviloba* are particularly slender and rarely exceed 7 mm in diameter. Plants may be very rhizomatous, with underground stems up to 150 mm long, which is remarkable in comparison to their thickness. The erect pieces protruding from the soil are often no more than 25 mm long. The shortness of these stems, their slenderness and their darkish colour make the plants very inconspicuous. The rhizomatous habit seems to be the species' response to arid, stony conditions with shallow soils (as also seen in *Tromotriche revoluta*), since plants growing in more sandy situations,

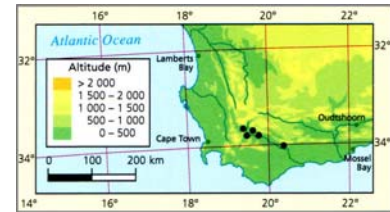


Fig. 17.3. Distribution of *Stapeliopsis breviloba*.

where the surrounding vegetation is denser, have longer stems above the soil. These stems are aggregated into clumps and have far less of a tendency to spread underground.

When in flower, *S. breviloba* is quite unmistakable. The peduncle often develops under the surface of the soil and then the flowers may be partially submerged. Generally the flowers are not longer than 13 mm, so they are quite small and they are ellipsoidal in shape. Their exterior is a somewhat shiny pinkish brown with numerous fine and longitudinal, translucent lines. The lobes are shorter than in any other species in the genus and always remain joined at the tips. If the flower is opened up, the inside will be found to be bi-coloured, being pale around the mouth of the tube and on the lobes and deep maroon below this, continuing to the base. There are many bristles in the lower half of the tube, a few of them arising from slightly raised papillae.

The deep maroon corona is similar to that of other species such as *S. saxatilis*. Our combined morphological and molecular results (Bruyns *et al.* 2005) show that *S. saxatilis* and *S. breviloba* are sister species.

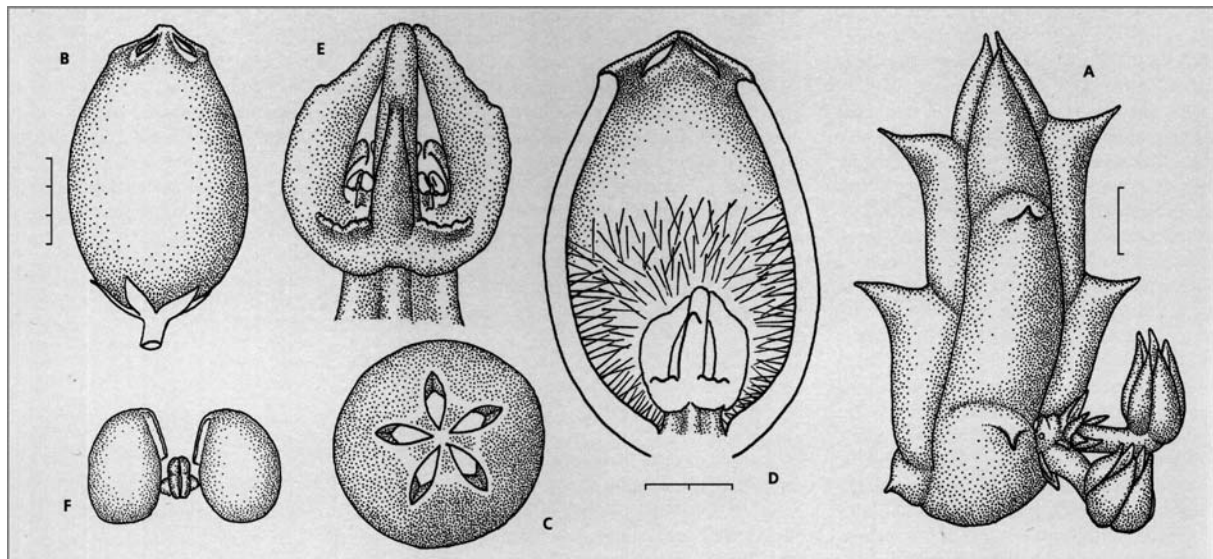


Fig. 17.4. *Stapeliopsis breviloba*. A, young stem with inflorescence. B, side view of flower. C, face view of flower. D, side view of dissected flower. E, side view of gynostegium. F, pollinarium. Scale bars: A, 2 mm; B, C, 3 mm (at B); D, 2 mm; E, 1 mm (at D); F, 0.25 mm (at D). Drawn from PVB 1704, Sandberg, Worcester.

History

It is not quite clear who discovered *S. breviloba*. It was figured (under the unpublished name *Pectinaria villettii*) by Lückhoff (1952), so Charles T. Villett must have found it a little before Lückhoff's book appeared. P.A. Brand van Breda of the Worcester Veld Reserve, which is attached to the Department of Agriculture, also obtained plants around this time and his collection flowered in 1952 in Pretoria. It was on this material that the name *Pectinaria breviloba* was based.



Fig. 17.5. *S. breviloba*, PVB 1704, Sandberg, Worcester.



Fig. 17.6. *S. breviloba*, PVB 964, south of Worcester, in habitat, May 1978.



Fig. 17.7. *S. breviloba*, PVB 1704, Sandberg, Worcester.



Fig. 17.8. *S. breviloba*, PVB 1704, Sandberg, Worcester.

2. *Stapeliopsis saxatilis*

Stapeliopsis saxatilis (N.E.Br.) Bruyns, Cact Succ. J. Gr. Brit. 43: 77 (1981).

Pectinaria saxatilis N.E.Br., Gard. Chron. Ser. 3, 35: 211 (1904).

Neopectinaria saxatilis (N.E.Br.) Plowes, Excelsa 20: 12 (2003).

Type: South Africa, Cape, Zout Kloof, N.S. Pillars 115 (K, holo.; BOL, iso.).

Pectinaria tulipiflora C.A.Lückh., S. African Gard. & Country Life 24:101 (1934).

Neopectinaria saxatilis var. *tulipiflora* (C.A.Lückh.) Plowes, Excelsa 20:12 (2003).

Type: Cape, Vanrhynsdorp at foot of Bokkeveld Mountains, J. Lückhoff sub Lückhoff 112 (missing).

Lectotype (designated here): A.C. White & B. Sloane, *Stap.*, ed. 2, 2: t. XIX, opp. p. 734.

Dwarf non-rhizomatous succulent forming mat up to 300 mm diam. **Stems** 25-300 mm long, 8-25 mm thick, prostrate, glabrous, initially pale grey-green later often yellowish or reddish green sometimes speckled with purple-red; **tubercles** 2-5 (-8) mm long, broadly conical, slightly laterally flattened and joined near base into 4 acute angles along stem between which stem concave, tapering to sharp yellow-tipped conical spreading tooth. **Inflorescences** glabrous, 1 (-3) per stem, with 1-10 flowers developing above surface of soil on knobby peduncle up to 5 mm long; **pedicel** 3-12 mm long, 1 mm thick, ascending and holding flower facing upwards; **sepals** 2-3 mm long, 1 mm broad at base, ovate-lanceolate, acuminate, often with recurved tips. **Corolla** 8-21 mm long, 6-11 mm diam., ellipsoidal to obovoid or obconical if lobes free; outside glabrous, ± shiny, dark maroon to dark red; inside velvety maroon, red to yellowish pink or pale pink.



Fig. 17.9. *S. saxatilis*, PVB 7110, south-west of Willowmore.

STAPELIOPSIS SAXATILIS

with many erect straight white bristles from near tips of lobes to near base of tube, towards the base some arising from low conical papillae; **tube** 6-15 mm long, 4-6 mm broad, cupular or widening towards mouth from narrow base, walls less than 0.5 mm thick; **lobes** 4-9 mm long, 4-7 mm broad at base, ascending-connivent and fused at tips to ascending-spreading and free at tips, ovate-deltate to narrowly deltate, acute. **Corona** 3-4 mm tall, 2-3 mm broad, raised on very short stout obtusely pentagonal stipe, shiny dark maroon to pale yellow; **outer lobes** < 0.5 mm long, ascending-spreading, truncate to emarginate, forming shallow pouch between bases of inner lobes and fused laterally to them for entire length; **inner lobes** 2.0-3.5 mm long, erect then connivent at apices, laterally flattened in lower half becoming $\pm$ terete and sometimes tuberculate above, usually with prominent to obscure obtuse $\pm$ deltoid dorsal projection near middle.

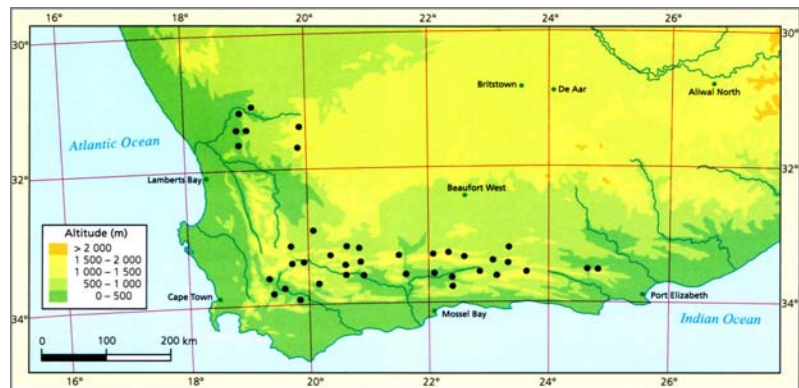


Fig. 17.10. Distribution of *Stapeliopsis saxatilis*.

Distribution and habitat

Stapeliopsis saxatilis is the most widely distributed species in the genus and is known from somewhat north-east of Vanrhynsdorp on the southern boundary of Namaqualand to near Uitenhage.

The species is found widely in the Worcester-Robertson Karoo and Little Karoo, and it grows at the southern edge of the Great Karoo from Laingsburg to east of Prince Albert along the northern slopes of the Swartberg.

From Worcester to Willowmore it occurs fairly frequently. East of Willowmore it is found in a few isolated spots, mainly on the lower slopes of the sandstone mountains, as far east as Cockscomb Peak to the south of Steytlerville. There are a few isolated records from the Ceres Karoo. Considerably further to the north it has been found quite widely from Vanrhyn's Pass in the west to south-east and north-east of Calvinia as well as up to about 50 km north of

Nieuwoudtville. This part of the distribution appears to be disjunct from the remainder further south.

Plants are almost always found on stony slopes and are especially associated with dense stands of *Crassula rupestris* subsp. *rupestris*, which is often the dominant plant on north-facing shale slopes in the Little Karoo. From the Anysberg and eastwards as far as the Groot Winterhoek Mountains it also grows

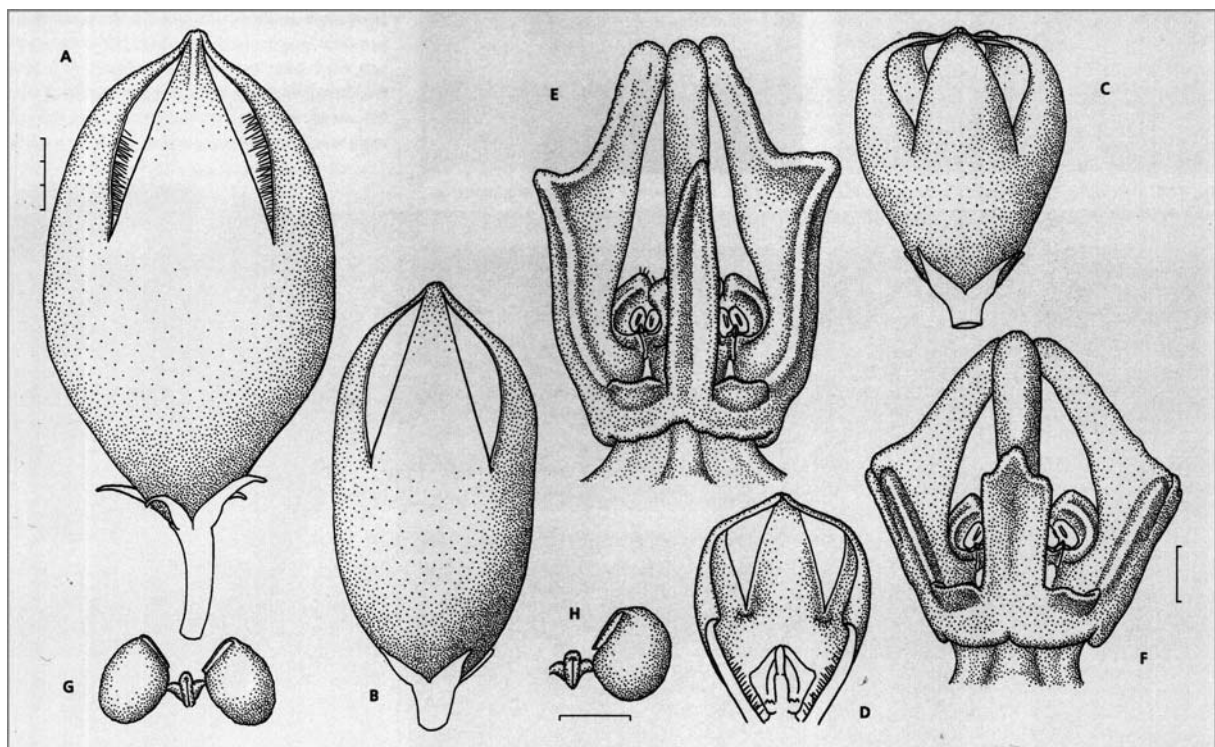


Fig. 17.11. *Stapeliopsis saxatilis*. A-C, side view of flower. D, side view of dissected flower. E, F, side view of gynostegium. G, H, pollinarium. Scale bars: A-D, 3 mm (at A); E, F, 0.5 mm (at F); G, H, 0.25 mm (at H). Drawn from: A, E, G, PVB 2419, Ribbokkop, south-east of Touws River; B, PVB 2544, Meideberg, eastern Ceres Karoo; C, D, F, H, PVB 2428, Buffelsrivierpoort, south of Laingsburg.



Fig. 17.12. *S. saxatilis*, PVB 4905, north-west of Willowmore.



Fig. 17.13. *S. saxatilis*, PVB 6244, Kareedouw, between Klaarstroom and Prince Albert, with nearly spherical flowers.



Fig. 17.14. *S. saxatilis*, PVB 2419, Ribbokkop, south-east of Touws River.

in soils derived from sandstones. In these situations it is associated with *Crassula rupestris*, the small fern *Cheilanthes hirta* or tufts of grass, and grows in small pockets of soil among rocks and bushes or on exposed slabs of rock.

Diagnostic features and relationships

The stems of *S. saxatilis* are mostly prostrate and partially (rarely wholly) buried in leaf-litter and among small stones on the surface of the soil. They may be erect initially but soon arch back to the soil. They are usually grouped together into dense, often very tightly packed mats. Individually they are very variable in length, but some can reach 300 mm on occasion. They are also very variable in thickness, even on one plant and sometimes on a single stem. The tubercles on the stem are joined into four low to sometimes quite boldly wing-like angles along the stems, often with the stem somewhat concave between them. Each tubercle is tipped with a tooth, which becomes yellow and quite hard with age. Mostly the stems are grey-green to reddish without any markings, but in plants growing in sandstones in the south-eastern Cape they are mottled with irregular purple-red blotches. In these plants, also, the surface is more papillate than usual.

In *S. saxatilis* flowers are produced on short peduncles near the bases of the stems, usually on the sides or on the undersurface of the stem (if it is prostrate) and only rarely on its upper surface. They are extremely variable in shape and size, from short and nearly spherical to ellipsoidal, in the latter case often with a distinctly inflated base. The tube may occupy anything from less than half the length of the flower to most of its length and occasionally it has little inwardly folded patches just below the bases of the lobes. The lobes normally remain joined at their tips. In material from north and west of Nieuwoudtville they do sometimes become detached apically and then the shape of the corolla is rather different, resembling an inverted cone. This difference in shape was partly responsible for the description of *Pectinaria tulipiflora* by Lückhoff. Mostly the



Fig. 17.15. *S. saxatilis*, PVB 2428, Buffelsrivierpoort, south of Laingsburg. The mottled stems can just be seen in this plant and in fig. 17.12.



Fig. 17.16. *S. saxatilis*, PVB 7333, Plathuis, Little Karoo, in habitat with a seedling of *Euphorbia pillansii* to the left, September 1997, showing the characteristically 4-angled stems.

STAPELIOPSIS STAYNERI



Fig. 17.17. *S. saxatilis*, PVB 6022, Kalkgat, north-east of Vanrhynsdorp, with some lobes free at their tips.



Fig. 17.18. *S. saxatilis*, PVB 6296, north-east of Calvinia.

flower is maroon or red outside and maroon inside, but sometimes the inside is yellowish. Larger, darker flowers usually have a dung-like odour; smaller flowers seem to have no detectable odour.

The inside of the flower has many straight white bristles, not densely clustered but evenly spread over the whole surface. These are longest around the bases of the lobes and become shorter towards their apices and towards the base of the tube where they sometimes also arise on a small papilla. The surface between the bristles is velvety from fine, spike-like epidermal cells and this lends it a very rich texture.

The corona is also extremely variable. This is especially true for the length of the inner lobes, the size and prominence of their dorsal projections and for the ridges running down from these projections. The whole structure is usually dark maroon but it may be yellow, especially in plants from west and north of Nieuwoudtville.

History

Stapeliopsis saxatilis was discovered in November 1902 by N.S. Pillans a little to the north of Laingsburg. An additional name, *Pectinaria tulipiflora*, was described by Carl Lückhoff in 1934 for material collected by his father, James Lückhoff, near Vanrhyn's Pass. He had found only two plants but today *S. saxatilis* is known to occur fairly widely in this area.

3. *Stapeliopsis stayneri*

Stapeliopsis stayneri (M.B.Bayer) Bruyns, *Aloe* 39: 82 (2003).

Pectinaria stayneri M.B.Bayer, *J. S. African Bot.* 41: 166 (1975).

Stapeliopsis saxatilis subsp. *stayneri* (M.B.Bayer)

Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 79 (1981).

Neopectinaria stayneri (M.B.Bayer) Plowes, *Excelsa* 20:12 (2003).

Type: South Africa, Cape, about 8 km inland from Infanta on bank of Breede River, *Stayner* sub KG 731/71 (NBG).

Dwarf non-rhizomatous succulent forming mat up to 300 mm diam. **Stems** 25-300 mm long, 8-10 mm thick, prostrate, glabrous, initially pale grey-green later often yellowish or reddish green sometimes speckled with purple-red; **tubercles** 2.5 (-8) mm long, broadly conical, slightly laterally flattened and joined near base into 4 acute angles along stem between which stem concave, tapering to sharp yellow-tipped conical spreading tooth. **Inflorescences** glabrous, 1 (-3) per stem, with 1-10 flowers developing above surface of soil on knobby peduncle up to 5 mm long; **pedicel** 3-12 mm long, 1 mm thick, ascending and holding flower facing upwards; **sepals** 2-3 mm long, 1 mm broad at base, ovate-lanceolate, acuminate, often with recurved tips. **Corolla** 8.5-9.0 mm long, 5-6 mm diam., obconical and widest about halfway down lobes; outside glabrous, $\pm$ shiny, dark flesh-coloured to pale pink becoming whitish near base; inside pink on lobes changing to pale yellow in lower half of tube, with many erect straight white bristles $\pm$ 0.5 mm long in lower half of tube only; **tube** 4-6 mm long, 3.0-4.5 mm broad, cupular but widening slightly towards mouth from narrow base, walls less than 0.5 mm thick; **lobes** 4-6 mm long, $\pm$ 3 mm broad at base, occasionally united at tips, narrowly deltate, acute. **Corona** 3-4 mm tall, 2-3 mm broad, raised on very short stout obtusely pentagonal stipe, yellow becoming reddish towards tips of inner lobes; **outer lobes** < 0.5 mm long, ascending-spreading, truncate to emarginate, forming shallow pouch between bases of inner lobes and fused laterally to them for entire length; **inner lobes**

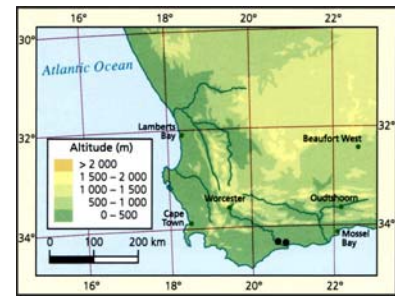


Fig. 17.19. Distribution of *Stapeliopsis stayneri*.

2.5-3.5 mm long, erect then connivent at apices, laterally flattened in lower half becoming $\pm$ terete above, dorsal projection $\pm$ absent.

Distribution and habitat

Stapeliopsis stayneri is found south of the Langeberg to the south and south-east of Swellendam and is restricted to the lower 20 km of the Breede River and a few patches along the Duiwenhoks River.

Plants of this species inhabit dry, rocky, usually steep, north- or east-facing, shale slopes with *Crassula rupestris* subsp. *rupestris*, *Euphorbia heptagona* and other succulents. Such habitats form locally arid, karroid enclaves surrounded by *renosterveld*.

Diagnostic features and relationships

Plants of *S. stayneri* also form dense mats (up to 300 mm in diameter) of tightly packed, mostly prostrate stems as is usually found in *S. saxatilis*. The stems are not as variable as in *S. saxatilis* and, while they may also reach 300 mm long, they rarely exceed 10 mm thick. They are usually greyish to reddish green.



Fig. 17.20. *S. stayneri*, PVB 1263, about 5 km north of the mouth of the Breede River.



Fig. 17.21. *S. stayneri*, PVB 1263, about 5 km north of the mouth of the Breede River.

The flowers of *S. stayneri* differ in several respects from those of *S. saxatilis*. They do not emit an unpleasant odour, but rather one resembling that of a beehive (Bayer 1975); nor are they as darkly coloured as those of *S. saxatilis*. Outside they are pink to dull flesh-coloured changing to whitish near the base. Inside, the colour is the same except that it becomes yellowish towards the base of the tube around the corona. The corolla is broadest a little beyond the mouth of the tube, so the tube is quite a bit narrower than the cage formed by the lobes. Instead of having bristles over most of the inside of the corolla, as is found in *S. saxatilis*, in *S. stayneri* these bristles are restricted to the lower, paler area around the corona. There are also occasionally a few short, dark ones near the margins of the lobes. The inside of the flower does not have the velvety appearance of *S. saxatilis* as the outer walls of the epidermal cells are rounded and short rather than long

and pointed.

In *S. stayneri* the corona is again rather variable in shape but is always bright yellow towards the base and becomes reddish towards the tips of the lobes. It is raised above the base of the tube on a very short stipe (shorter than in *S. saxatilis*). There are never any dorsal horns on the backs of the inner lobes, as are usually found in *S. saxatilis*.

In Bruyns (1981a) *S. stayneri* was treated as a subspecies of *S. saxatilis*. However, our combined morphological and molecular analysis of *Stapeliopsis* (Bruyns et al. 2005) showed that this is not correct and that *S. stayneri* is the sister species of *S. pillansii*.

History

Stapeliopsis stayneri was discovered by Frank J. Stayner in 1971 near the mouth of the Breede River alongside the Potberg.

4. *Stapeliopsis pillansii*

Stapeliopsis pillansii (N.E.Br.) Bruyns, *Cact. Succ.*

J. Gr. Brit. 43: 81 (1981).

Pectinaria pillansii N.E.Br., *Fl. Cap.* 4 (1): 869 (1909).

Neoplectinaria pillansii (N.E.Br.) Plowes, *Excelsa* 20: 12 (2003).

Type: South Africa, Cape, Glen Avon Estate, Somerset East, N.S. Pillans 180 (K, holo.; BOL, iso.).

Dwarf non-rhizomatous succulent forming mat up to 150 mm diam. **Stems** 20-150 mm long, 15-20 mm thick, prostrate, glabrous, grey to purplish above, paler and often pinkish below; **tubercles** 2-5 mm long, conical and joined into 4 obtuse angles along stem when young, later stem swelling to become $\pm$ convex between 4 rows of tubercles of which only an acute hardened pale yellow spreading to slightly recurved tooth remains. **Inflorescences** glabrous, 1 (-3) per stem, usually developing on underside of stems at or just below surface of soil on short knobby peduncle up to 5 mm long; **pedicel** 2-3 mm long, 1 mm thick, reddish, descending or spreading holding flower facing horizontally or downwards; **sepals** $\pm$ 2 mm long, ovate-lanceolate, acuminate, pinkish. **Corolla** 6-10 mm long, (7-) 12-14 mm diam., pear-shaped to campanulate; outside glabrous, smooth, red to maroon; inside red to maroon, with many erect straight white bristles up to 0.5 mm long from tips of lobes to base of tube (longest around mouth) but without basal papillae; **tube** 2-4 mm long, $\pm$ 4 mm broad, pentagonal, V-shaped with lower part closely enclosing base of gynostegium and stipe, walls 1.5-2.0 mm thick from near base to mouth; **lobes** $\pm$ 4 mm long, 4-6 mm broad at base, ascending and remaining connate at tips to erect or widely spreading, deltate, acute, thick and rigidly fleshy. **Corona** 2.5-3.0 mm tall, $\pm$ 3.5 mm broad, raised on stout obtusely pentagonal stipe $\pm$ 1 mm long, dark maroon with blackish edges; **outer lobes** $\pm$ 1 mm long, ascending-spreading, channelled above, narrowing slightly to truncate or emarginate apex, fused laterally to inner lobes only near base; **inner lobes** 2.3-3.0 mm long,

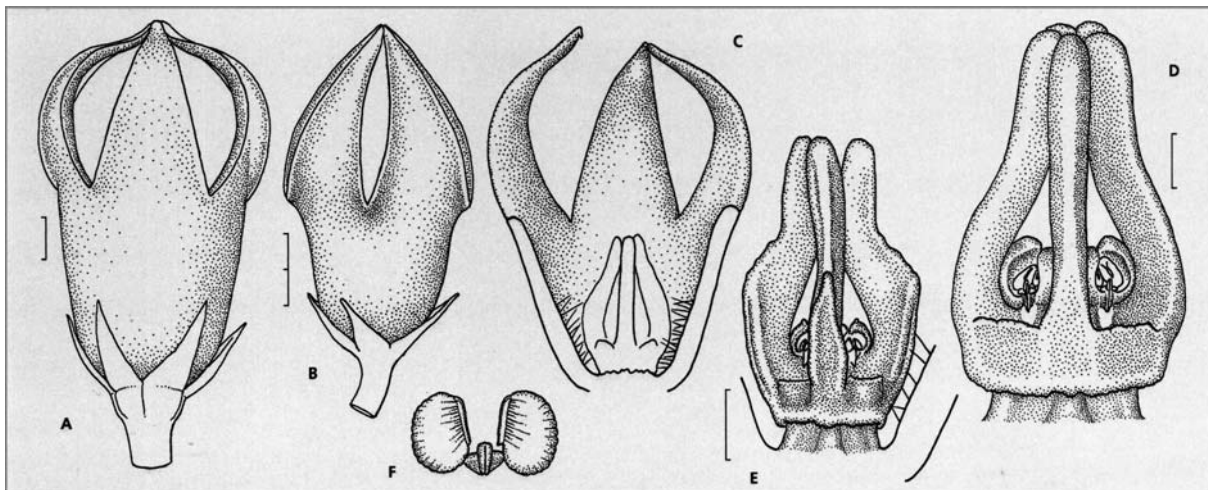


Fig. 17.22. *Stapeliopsis stayneri*. A, B, side view of flower. C, side view of dissected flower. D, E, side view of gynostegium. F, pollinarium. Scale bars: A, C, 1 mm (at A); B, 2 mm; D, 0.5 mm; E, 1 mm; F, 0.25 mm (at E). Drawn from: A, C, D, F, PVB 1262, east bank of Breede River, near Infanta; B, E, PVB 6262, Duiwenhoks River.

STAPELIOPSIS PILLANSII

erect then connivent at apices, laterally flattened becoming dorsiventrally flattened or terete near obtuse slightly swollen tips, with slight to prominent obtuse spreading $\pm$ deltoid dorsal wing near middle.

Distribution and habitat

As seems to be typical in this genus, *S. pillansii* has a fairly wide distribution but is uncommon. It occurs in the south-eastern part of the Great Karoo and has been collected from west of Rietbron in the west sporadically eastwards to near Somerset East, Kommadagga and Port Elizabeth. The only area where it seems to be reasonably frequent is between Somerset East, Pearston and Jansenville but even here plants are very scattered and a recent search lasting over two hours turned up only four specimens.

Plants are usually few at any one locality and have almost always been observed growing on low, stony ridges or flat gravelly areas under small shrubs. These protective shrubs may be anything from *Lycium* or small composites to the dense, spiny mounds of *Euphorbia ferox*, where the stems hide around the bases of those of the *Euphorbia*.

Diagnostic features and relationships

The stems of *S. pillansii* are prostrate and are usually nearly 20 mm thick. They bear considerable superficial resemblance to stems of *S. saxatilis*, but several subtle differences can be observed if they are examined closely. They

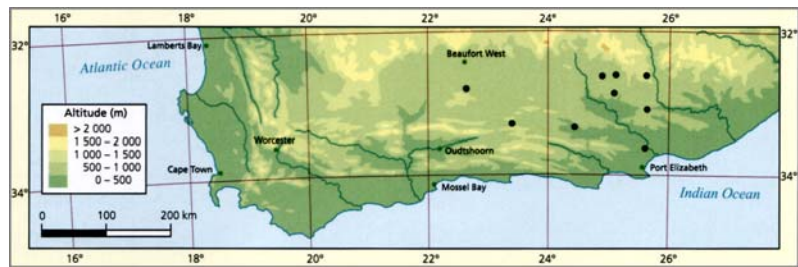


Fig. 17.23. Distribution of *Stapeliopsis pillansii*.



Fig. 17.24. *S. pillansii*, PVB 1805, south-west of Pearston, in habitat, December 1978.

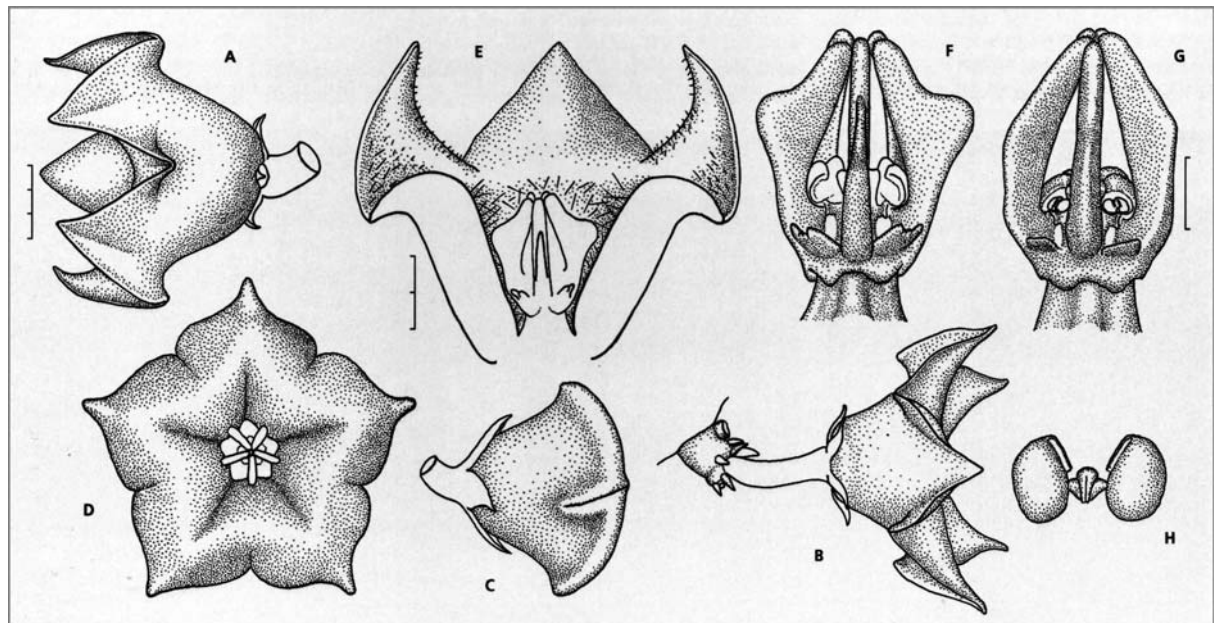


Fig. 17.25. *Stapeliopsis pillansii*. A, B, side view of flower. C, bud. D, face view of flower. E, side view of dissected flower. F, G, side view of gynostegium. H, pollinarium. Scale bars: A-D, 3 mm (at A); E, 2 mm; F, G, 1 mm (at G); H, 0.25 mm (at G). Drawn from: C, PVB 1805, south-west of Pearston; rest, PVB 1589, Pearston.

have a harder, shinier epidermis (where the cells have more or less entirely flat outer walls) with more conical, slightly recurved tubercles. The tubercles are fused into four angles along the stem when it is young but as they mature there remain only four rows of teeth along the stem without any sign of the join between the tubercles. When turgid, the stem becomes convex whereas in *S. saxatilis* it remains somewhat concave.

Stapeliopsis pillansii mainly produces its flowers beneath the soil and only on lifting up a plant will they usually be seen. Peduncles are produced on both the upper and lower sides of the stem but usually only those on the lower surface mature to produce flowers. Flowering seems to be especially prolific in loose soil with a high leaf-mould content (Bayer, pers. comm.).

In all the other species the flowers are urceolate and are held erect by the pedicels. In *S. pillansii* the flowers are campanulate if the lobes spread out, or they are bud-like and more or less pear-shaped if the lobes remain close together towards their tips. The flowers are held facing horizontally or downwards. The entire flower is a deep maroon and this colour continues into the pedicels and the peduncle. Both the corolla lobes and the tube are unusually thick, rigid and fleshy. In the other species, the tube is circular in cross-section and is quite broad towards the base, thus remaining some distance away from the gynostegium. In *S. pillansii* it is strongly pentagonal and its sides are close to the gynostegium.



Fig. 17.26. *S. pillansii*, PVB 5070, west of Rietbron.

The corona is somewhat darker than the rest of the flower and the lobes are edged with blackish. They have a very similar shape to those in *S. saxatilis*.

History

A single plant of this remarkable species was discovered by N.S. Pillans in July 1903 on the Glen Avon Estate just outside Somerset East. It was many years before it was collected again. The next two records were made in February 1937, one near Pearston by Eve Palmer and another at Addo. A further specimen was collected by Ronald James near Port Elizabeth in 1938. Only a few more collections have been made since then.



Fig. 17.27. *S. pillansii*, PVB 5070, west of Rietbron. The pale undersides of the stems are normally beneath the soil and have been lifted up to reveal the flowers.

5. *Stapeliopsis exasperata*

Stapeliopsis exasperata (Bruyns) Bruyns, *Cact. Succ. J. Gr. Brit.* 43: 82 (1981).

Pectinaria exasperata Bruyns, *J. S. African Bot.* 44: 153 (1978).

Hermanschwartzia exasperata (Bruyns) Plowes, *Excelsa* 20:17 (2003).

Type: South Africa, Cape, 20 miles north of Calvinia, Bruyns 1345 (NBG).

Dwarf rhizomatous succulent forming clump to 150 mm diam. **Stems** 10-60 (-100) mm long, 8-15 mm thick, decumbent, erect above soil often from horizontal subterranean runner up to 150 mm or more long, glabrous, grey-green, smooth (to naked eye); **tubercles** 2-4 mm long, conical, slightly laterally flattened and joined near base into 4 obtuse angles along stem, tapering to deltoid spreading tooth somewhat flattened above and subtended by 2 stipular denticles. **Inflorescences** glabrous, 1-4 per stem, usually developing beneath surface of soil, each with 1-10 flowers; **pedicel** 2-5 (-10) mm long, 1 mm thick, spreading with ascending apex holding flower facing upwards; **sepals** 2-3 mm long, 1 mm broad at base, lanceolate, acute, often with recurved tips. **Corolla** 16-28 (-32) mm long, 18-25 mm diam., ± cylindrical with lobes spreading at mouth of tube; outside glabrous, smooth, pinkish red to cream; inside pale pinkish to cream or white with dark maroon patch in base, with somewhat cylindrical obtuse bristly papillae on lobes (from base at least to middle) and in tube, largest around mouth of tube and base of lobes (becoming very short towards base of tube) each with an apical bristle, bristle increasing to 1 mm long towards base of tube; **tube** 10-18 mm long, 4-7 mm broad, cylindrical, often widest near base and narrowing slightly towards mouth; **lobes** 6-16 mm long, 2.0-4.5 mm broad at base, usually widely spreading but occasionally remaining fused at tips, lanceolate-acuminate, without thickening in corolla around mouth. **Corona** 3.0-3.5 mm tall, 3-4 mm broad, raised on very short yellow obtusely pentagonal stipe, dark maroon; **outer lobes** ascending, broadly obtusely bifid near apex, < 0.5 mm long, forming shallow pouch between bases of inner lobes and fused laterally to them for entire length; **inner lobes** ±2.5 mm long, erect then connivent at apices, laterally flattened becoming dorsiventrally flattened near obtuse slightly swollen tips, with prominent obtuse spreading ± deltoid dorsal wing near middle.

Distribution and habitat

Stapeliopsis exasperata is found from Loeriesfontein to near Sutherland at altitudes of 900-1100 m and it also occurs around Matjiesfontein and among the mountains from Montagu to Barrydale at between 800 and 950 m.

Plants grow in flattish areas that may sometimes be somewhat stony. Here they are found under small bushes, usually in small accumulations of leaf-litter and loose soil where the subterranean inflorescences and partially underground flowers can develop more easily. However, they have been seen in very hard ground too, but are then not at all common.

STAPELIOPSIS EXASPERATA

Diagnostic features and relationships

Vegetatively, *S. exasperata* is distinctive. In the field, plants form clumps up to 150 mm across of very short (15–25 mm long), erect, pyramidal stems. All these stems are joined beneath the surface and the plant often has also one or two spreading runners around its edges. On these runners the horizontally spreading, underground parts are slender and rounded but become abruptly thicker just before emerging from the soil. The stem which then appears above the surface is erect, square, often narrowing towards the apex like a pyramid, with very small, deltoid teeth, each of which is subtended by two quite obvious, stipular denticles (fig. 17 G).

In *S. exasperata* the peduncles arise around the bases of the stems which is nearly always beneath the surface of the soil and sometimes as much as 25 mm below its surface. Consequently the flowers are usually at least partially submerged at anthesis. Very occasionally they are completely beneath the surface of the soil but usually at least the lobes project from the ground, rather like minute versions of the flowers of the parasitic genus *Hydnora*. Very occasionally the lobes are joined at their tips but normally they are free and spread out horizontally on the surface of the soil.

The outside of the flower is reddish (with the intensity depending on how exposed the

flower is - those wholly beneath the surface usually remaining cream or pale pink) which develops from a relatively bright green in the buds. The inside of the flower is usually pale pink on the lobes and for most of the tube, from which it suddenly changes to dark maroon in the base of the tube, at the height of the top of the corona. While the outside is smooth and somewhat shiny, the inside is rough and bristly with quite tall papillae which reach their greatest length around the bases of the lobes and mouth of the tube, becoming very gradually shorter towards the base of the tube. Towards the tips of the lobes they also become shorter and rapidly decrease in number. In the dark maroon patch in the base of the tube, the apical cell of each papilla becomes elongated into a bristle. Elsewhere this apical bristle is not distinguishable from the other epidermal cells of the papilla (except if greatly magnified). The surface between all these papillae is crystalline and velvety from fine, spike-like epidermal cells and the same spike-like cells cover the papillae to give them a finely furry appearance.

The corona has a dark maroon colour, which exactly matches that of the dark patch in the base of the tube. It is no different in shape and structure from that in species such as *S. saxatilis*.

Florally *S. exasperata* could not be confused with any other species: the lanceolate, slenderly tapering corolla lobes with prominent papillae on their inner surface and the more or less

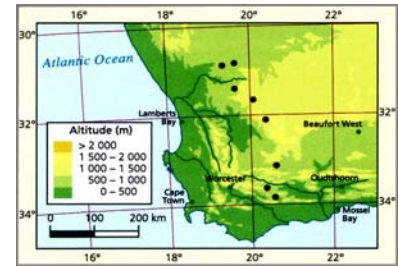


Fig. 17.28. Distribution of *Stapeliopsis exasperata*.

cylindrical tube are sufficient to separate it from all the other species.

In our combined morphological and molecular analyses (Bruyns *et al.* 2005) *S. exasperata* is sister to all the other southern species (*S. breviloba*, *S. pillansii*, *S. saxatilis* and *S. stayneri*) but the relationship is poorly supported.

History

The earliest collections of *S. exasperata* showed already that the species is comparatively widely distributed. It was first recorded from near Loeriesfontein in 1940 by Marthinus Lawrence Malherbe (24 October 1885–13 March 1976), who was the founder of the well-known succulent nursery 'Sheilam' near

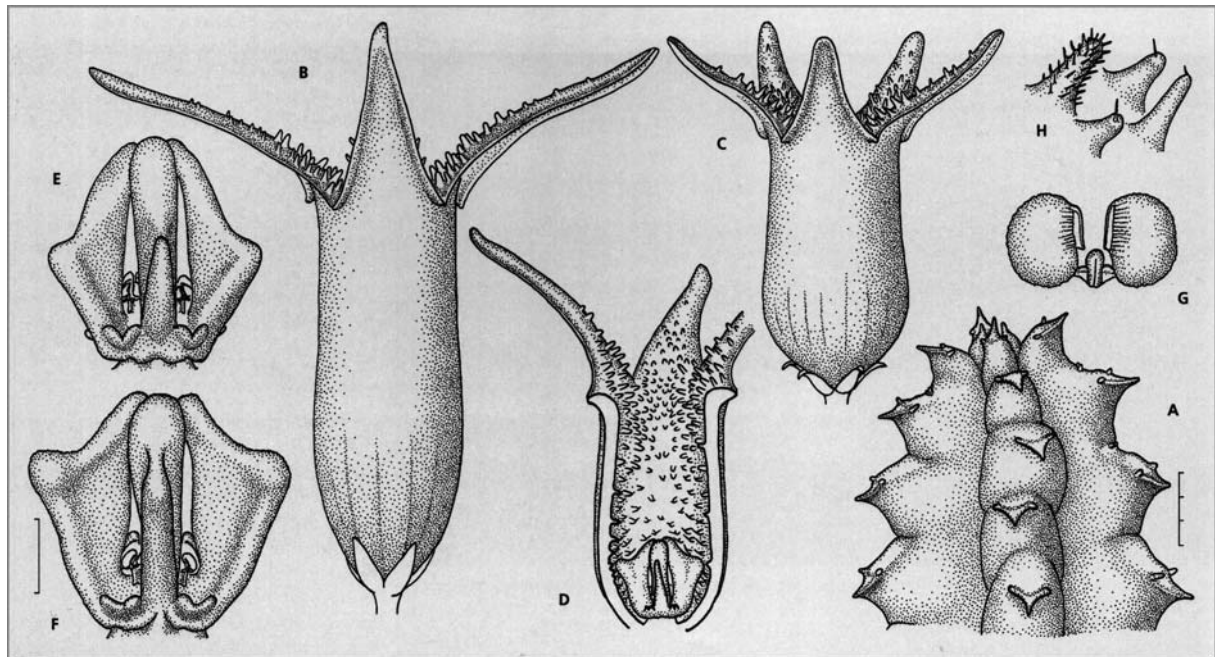


Fig. 17.29. *Stapeliopsis exasperata*. A, apex of stem. B, C, side view of flower. D, side view of dissected flower. E, F, side view of gynostegium. G, pollinarium. H, papillae inside corolla: 3 tall ones from mouth of tube, all spinescent as in leftmost; shorter one from base of tube, not as spinescent as others. Scale bars: A–D, 3 mm (at A); E–F, 1 mm (at F); G, 0.25 mm (at F); H, 0.5 mm (at F). Drawn from PVB 1345, north-west of Calvinia.

Robertson. The next collection was made by H. Hall in 1953 east of Montagu and in 1956 it was recorded from Matjiesfontein by Charles T. Villet. Specimens and paintings of these collections remained unidentified in the herbaria at Kirstenbosch and the University

of Cape Town. It was described in 1981 from material found quite fortuitously near Calvinia by the present author in July 1976. Today only a few more localities have been added, especially south-east of Calvinia and much further south near Barrydale.



Fig. 17.30. *S. exasperata*, PVB 5078, Matjiesfontein. The flower to the left is almost completely submerged.



Fig. 17.31. *S. exasperata*, PVB 5078, Matjiesfontein, showing extent of underground growth (white) and flowers arising from it.



Fig. 17.32. *S. exasperata*, PVB 2820, west of Barrydale.



Fig. 17.33. *S. exasperata*, PVB 4306, north-west of Calvinia.

6. *Stapeliopsis urniflora*

Stapeliopsis urniflora Lavranos, J. S. African Bot. 32:195 (1966), as '*S. urnaeiflora*'.

Type: Namibia, Tiras Mountains, *Lofty-Eaton* sub *Lavranos* 2536 (PRE).

Dwarf slightly rhizomatous succulent forming clump to 150 mm diam. **Stems** 20-70 (-200) mm long, 6-20 mm thick, decumbent with horizontal (and often quite slender) portion sometimes spreading up to 60 (-100) mm underground, silvery green to green with dark green to purplish mottling, minutely papillate (glabrous to naked eye); **tubercles** 1-3 mm long, broadly deltoid, laterally flattened and joined near base into 4 narrowly obtuse angles along stem, tapering abruptly to minute conical tooth. **Inflorescence** glabrous, usually developing at level of surface of soil or beneath it, with several lanceolate bracts up to 1 mm long on short broad peduncle (occasionally up to 30 mm long); **pedicel** 5-8 mm long, 1 mm thick, spreading then erect holding flower facing upwards; **sepals** 2.0-2.5 mm long, 1 mm broad at base, ovate-lanceolate, acuminate. **Corolla** 9-18 mm long, 5-11 mm diam., ovoid with somewhat flattened base; outside glabrous, smooth, shiny purple-red; inside paler velvety (matt) purple-red, densely covered with conical obtuse papillae on inside of tube only, longest (up to 0.5 mm) towards mouth and shortest towards base, each with an apical bristle (very short in upper half of tube, up to 2 mm long in lower half); **tube** 6-16 mm long, 8-10 mm broad near base narrowing to 2.0-2.5 mm inside slightly thickened mouth, ovoid; **lobes** 2.0-3.5 mm long, 2.0-2.5 mm broad at base, erect to spreading, deltoid, acute. **Corona** $\pm$ 3 mm tall, 4.0-4.5 mm broad, raised on circular stipe $\pm$ 1.5 mm long and 5-6 mm thick narrowing above into gynostegium, purplish red becoming yellowish at base of inner lobes, glabrous; **outer lobes** 1.0-1.5 mm tall, fused laterally with sides of inner lobes into cylindrical to bowl-shaped tube 3 mm broad at base and 3.0-4.5 mm broad around mouth, with pairs of nearly erect to



Fig. 17.34. Distribution of *Stapeliopsis urniflora*.

STAPELIOPSIS URNIFLORA

spreading deltate lobules 0.5-0.7 mm long at mouth of tube alternating with inner lobes; **inner lobes** 2.0-2.3 mm long, erect then connivent at broadly obtuse apices, laterally flattened, slightly broadened in lower half but otherwise without dorsal appendage.



Fig. 17.35. *S. urniflora*, Van Jaarsveld 11587, Tatasberg, Richtersveld.

Distribution and habitat

This very little-known species occurs in south-western Namibia and in the north-western corner of South Africa. In Namibia it is known in the Tiras Mountains south-west of Helmeringhausen, where it is not uncommon and has been gathered in several places, mainly towards their eastern flank. Further south it has been collected just south of Aus and in the dolomitic hills east of Witpütz, where it is also not uncommon. It has also been recorded from the eastern part of the Richtersveld. This gives it a relatively wide and diffuse distribution. However, like *S. exasperata*, it is very inconspicuous and so it may be more common than these scanty records indicate.

Plants are found growing on gneissic or dolomitic slopes. In these often quite steep habitats they shelter between stones or under small bushes and occasionally inside small tufts of grass.

Diagnostic features and relationships

Vegetatively one can usually tell *S. urniflora* and *S. neronis* apart. Stems of *S. neronis* are stouter and grow only on the surface of the soil. In *S. urniflora* most of the younger stems start off with a slender, spreading base and this can develop into an underground runner

up to 60 mm long or more, which is without obvious angles. Once this rises to the surface, it becomes strongly 4-angled and then it is much thicker and erect. The stems are short and relatively squat and form clumps up to 150 mm (rarely as much as 300 mm) in diameter. As in *S. neronis* they are transversely mottled with purplish or darker green, but in *S. urniflora* the background colour is often somewhat silvery. Their surface is also papillate but here the papillae are smaller than those in *S. neronis*. Consequently the stems are slightly shiny, glabrous to the naked eye and more or less smooth to the touch.

In *S. urniflora* the flowers are borne on small peduncles which are produced near the bases of the younger stems, often slightly beneath the soil. The erect corolla is relatively small at around 15 mm long. Most of it is made up of an ovoid tube with a somewhat flattened, broader base narrowing gradually towards the mouth. At the mouth of the tube there are five small, deltoid lobes which usually spread slightly. Outside, the corolla is glabrous, shiny and deep purple-red. The interior is a dull, slightly lighter purple-red. The tube is not thickened at the mouth, nor are the lobes different in colour to the remainder of the flower, as they are in *S. neronis*. The inside is covered with a forest of prominent papillae which, as usual, are larger towards the mouth of the tube and vanish towards the base. They are not found on the lobes at all. Each papilla has a modified

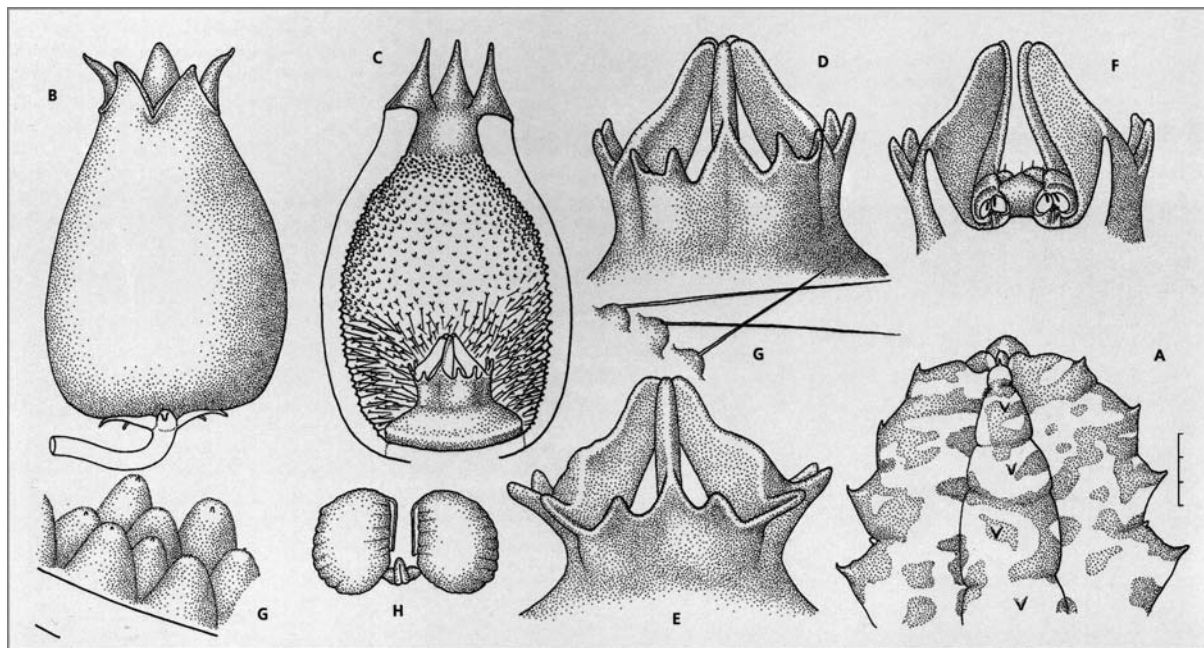


Fig. 17.36. *Stapeliopsis urniflora*. A, apex of stem. B, side view of flower. C, side view of dissected flower. D, E, side view of gynostegium. F, side view of gynostegium with one inner and two outer corona lobes removed. G, papillae inside corolla: those with long setae from base of tube; those with very short apical seta from just above middle of tube. H, pollinarium. Scale bars: A-C, 3 mm (at A); D-F, 1 mm (at A); G, 0.5 mm (at A); H, 0.25 mm (at A). Drawn from: E, PVB 5733, south-west of Helmeringhausen, Namibia; rest, PVB 1477, Tiras, south of Helmeringhausen, Namibia.

STAPELIOPSIS URNIFLORA

apical cell. Towards the mouth of the tube these apical cells are fashioned into a peculiar broad ridge embedded in the papilla but in the lower half of the tube they take the form of straight bristles that increase in length towards the base of the tube.

The gynostegium is seated on a pedestal-like stipe that is considerably broader towards its base than the gynostegium itself. The outer corona lobes are fused to the sides of

the inner lobes into a tube which slightly exceeds the height of the anthers. Each lobe is divided into two teeth at the top of this tube. The inner lobes are relatively broad and short and are strongly laterally flattened. In this respect the gynostegium of *S. urniflora* resembles the structures found in the species already discussed. The rhizomatous habit and often subterranean peduncle are particularly suggestive of affinities with *S. exasperata*. Our

combined morphological and molecular results (Bruyns *et al.* 2005) show that *S. urniflora* and *S. khamiesbergensis* are sister species, with the relationship well supported. The differences between them are discussed under the latter.

History

Stapeliopsis urniflora was first collected in the Tiras Mountains in September 1963, by W. Lofty-Eaton, a one-time collector of *Lithops* who farmed in the Maltahöhe district. In 1965 it was found again a little south of Aus by Roy Littlewood, who at that time was the assistant curator of the Karoo Botanic Garden in Worcester. Records have gradually accumulated since then. The species was believed to be endemic to Namibia (Bruyns 1981a, Plowes 1993) but this has proved to be erroneous as it has been found in the northern mountains of the Richtersveld, just inside the South African border.



Fig. 17.37. *S. urniflora*, PVB 5733, south-west of Helmeringhausen, Namibia, in habitat among granite rocks.



Fig. 17.38. *S. urniflora*, PVB 5733, south-west of Helmeringhausen.



Fig. 17.39. *S. urniflora*, PVB 1477, Tiras, south of Helmeringhausen, Namibia.

7. *Stapeliopsis khamiesbergensis*

Stapeliopsis khamiesbergensis Bruyns, Aloe 39:
82 (2003).

Type: South Africa, east of Springbok, Bruyns 8249
(BOL).

Small rhizomatous succulent to 300 mm diam. **Stems** 30–200 mm long, 3–20 mm thick, decumbent with horizontal (and often very slender) portion spreading up to 100 mm underground, silvery green to green with purplish mottling, minutely papillate (glabrous to naked eye); **tubercles** 1–3 mm long, broadly deltoid, laterally flattened and joined near base into 4 narrowly obtuse angles along stem, tapering abruptly to minute conical tooth. **Inflorescence** glabrous, usually developing at level of surface of soil or beneath it, with several lanceolate bracts up to 1 mm long on short broad peduncle (occasionally up to 30 mm long); **pedicel** 2–3 mm long, 1 mm thick, purplish, spreading then sometimes erect, holding flower facing upwards or outwards; **sepals** 3 mm long, 0.5 mm broad at base, lanceolate, acuminate, with spreading apices. **Corolla** 10–12 mm long, 5–7 mm diam., urceolate with somewhat flattened base; outside finely papillate, dull purple-maroon; inside maroon in tube, dull yellow on lobes, densely covered with conical obtuse papillae on inside of tube only, longest (up to 0.5 mm) towards mouth and shortest towards base, each with an apical bristle (very short in upper half of tube, up to 2 mm long in lower half); **tube** 10–12 mm long, 5–7 mm broad around middle narrowing to 2 mm inside slightly thickened mouth, ovoid; **lobes** 2.5 mm long, 1.5–2.0 mm broad at base, erect to spreading, deltoid, acute. **Corona** 5 mm tall, 5 mm broad, raised on low circular stipe < 1 mm long and $\pm$ 5 mm broad narrowing abruptly above into gynostegium, purplish red, glabrous; **outer lobes** $\pm$ 3 mm tall, fused laterally with sides of inner lobes into vase-shaped tube < 2 mm broad at base widening to 5 mm broad at apex, with pairs of nearly erect deltoid lobules 0.6 mm long at mouth of tube alternating with inner lobes; **inner lobes** 3 mm long, erect and then connivent at obtuse apices, laterally flattened, slightly broadened in lower half but otherwise without dorsal appendage.

Distribution and habitat

This species is only known from the Kamiesberg. Two collections have been made in the vicinity of Springbok and it is also recorded near Kamieskroon, on the western edge of Bushmanland.

In both spots where they were observed around Springbok, plants of *S. khamiesbergensis* were seen growing in dense clumps of *Polymita albiflora* on low and relatively bare sheets of gneiss. The larger specimens of *Polymita* appear to be the most important nurse-plants on many of these bare rock-sheets, providing shelter for a range of small succulents belonging to genera such as *Adromischus*, *Anacampseros*, *Crassula*, *Larryleachia*, *Stapelia* and *Stapeliopsis*. The ground beneath the larger clumps of *Polymita* is well supplied with a dense covering of leaf-litter and it is in this that occasional specimens of *Stapeliopsis* may be found to flourish. Most of the plant within the clump consists of very slender stems partially buried in this leaf-litter, the stems becoming stouter only where they peep out from among the twigs of the sheltering clump.

Diagnostic features and relationships

Stapeliopsis khamiesbergensis is, for the most part, vegetatively indistinguishable from *S. urniflora* in that the stems are similarly coloured and of similar dimensions. In *S. khamiesbergensis*, however, the basal horizontal part of the stem can be remarkably slender and is often considerably longer than has ever been observed in *S. urniflora*. The rhizomatous habit is frequently more pronounced in *S. khamiesbergensis*.

The flower in this species has often been found to emerge from a subterranean pedicel. The lower part of the corolla is also beneath the soil and only the upper part with the lobes projects out of the ground.

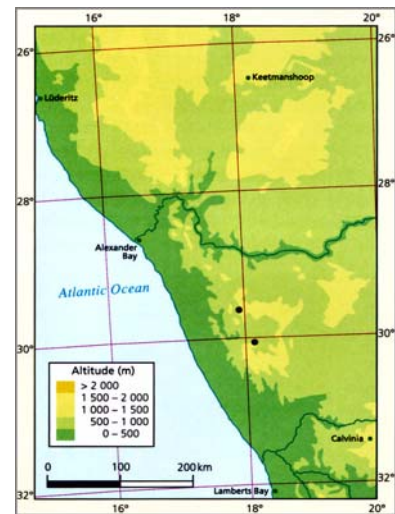


Fig. 17.40. Distribution of *Stapeliopsis khamiesbergensis*.

It is in subtle features of their flowers that these two species are most clearly distinct. In *S. urniflora* the exterior of the flower is always shiny and smooth. In *S. khamiesbergensis*, on the other hand, it is dull and papillate and, in this respect the surface is more like that in *S. neronis*. In addition, the inside of the rather narrower corolla lobes is dull yellow and different in colour from the rest of the inside of the tube. This contrasts with the uniformly purple-red inside of the corolla that is found in *S. urniflora*. Again in this respect, *S. khamiesbergensis* is reminiscent of *S. neronis*, where the inside of the corolla lobes has a very different colour from the rest of the flower. In *S. khamiesbergensis* the vase-shaped tube formed by the outer corona is considerably more substantial (in particular, taller) than that in *S. urniflora*, being about 3 mm tall and expanding from a

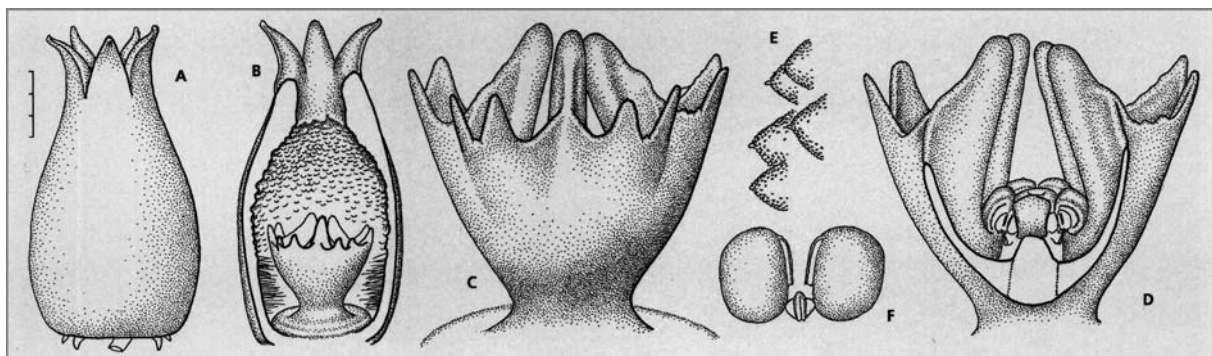


Fig. 17.41. *Stapeliopsis khamiesbergensis*. A, side view of flower. B, side view of dissected flower. C, side view of gynostegium. D, side view of gynostegium with one inner and two outer corona-lobes removed. E, papillae inside corolla from just above middle of tube. F, pollinarium. Scales: A–B, 3 mm (at A); C–D, 1 mm (at A); E, 0.5 mm (at A); F, 0.25 mm (at A). All drawn from PVB 8249, east of Springbok.

distinctly slender base, whereas in *S. urniflora* it does not exceed 1.5 mm tall and is more or less cylindrical, without a narrow base.

History

It appears that a species of *Stapeliopsis* has been at least informally known around Springbok since about 1950 (H.C. Kennedy, pers. com.). In 1988 I was given a collection of this new species that was made by David M. Cumming in the Kamiesberg to the east of Kamieskroon. While this plant thrived in cultivation, it proved remarkably reluctant to flower and did so for the first time in January 2003! In August 2000 I was fortunate enough to locate a few plants

east of Springbok and these flowered for the first time in April 2002 and again in January 2003. They showed that earlier suspicions that this material represented *S. urniflora* were mistaken and that they differed in sufficiently many features that a new species is justified. These differences have all proved to be present in Cumming's material as well. The existence of this new species shows that the flora of Nam-aqualand in general and of the Kamiesberg in particular is still relatively little-known, despite much collecting activity and even despite the research that was done to produce the booklet on the flora of the Kamiesberg by Adamson (1938).



Fig. 17.42. *S. khamiesbergensis*, PVB 8249, east of Springbok.

8. *Stapeliopsis neronis*

Stapeliopsis neronis Pillans, *S. African Gard. & Country Life* 18: 32 (1928).

Type: South Africa, Cape, Richtersveld, Annisfontein, *Nero* sub N.S. Pillans 5728 (BOL).

Small non-rhizomatous succulent forming clump 100-300 mm diam. **Stems** 40-150 (-300) mm long, 20-35 mm thick, decumbent, blue-green mottled with purple (grey on exposed parts), minutely pubescent; **tubercles** 1-4 mm long, broadly deltoid, laterally flattened and joined into 4 narrowly obtuse angles along stem, tapering abruptly to minute conical tooth. **Inflorescence** minutely pubescent, arising near base of stem on peduncle gradually elongating to 10 mm or more, with lanceolate bracts < 2 mm long; **pedicel** 5-10 mm long, $\pm$ 2 mm thick, spreading then erect holding flower facing upwards; **sepals** 2-4 mm long, ovate-lanceolate, acuminate, with recurved apices. **Corolla** 17-28 mm long, 11-16 mm diam., ellipsoidal to nearly spherical (narrowing $\pm$ equally to both ends); outside finely pubescent with acute papillae, deep purple usually with many darker longitudinal veins; inside velvety white on lobes and mouth of tube, deep purple below, densely covered with conical obtuse papillae on inside of tube only, longest (< 0.5 mm) towards mouth and disappearing towards base, each with apical bristle (very short in upper half of tube, up to 1.25 mm long towards base); **tube** 12-24 mm long, 13-15 mm broad at middle narrowing to 1.0-1.5 mm inside very much thickened mouth, ellipsoidal; **lobes** 4-5 mm long, $\pm$ 3 mm broad at base, erect to slightly spreading, narrowly deltoid, acute, very much thickened at base, with margins somewhat folded back so that inner surface strongly convex. **Corona** 7-11 mm tall, $\pm$ 5 mm broad, raised on circular stipe $\pm$ 2 mm long and 5-6 mm broad (only slightly broader than outer corona tube near base), dark purple; **outer lobes** 7-11 mm tall, fused into erect cylinder $\pm$ 5 mm broad which entirely hides rest of gynostegium, with 5 incurved broadly obtuse to emarginate flaps at mouth alternating with inner

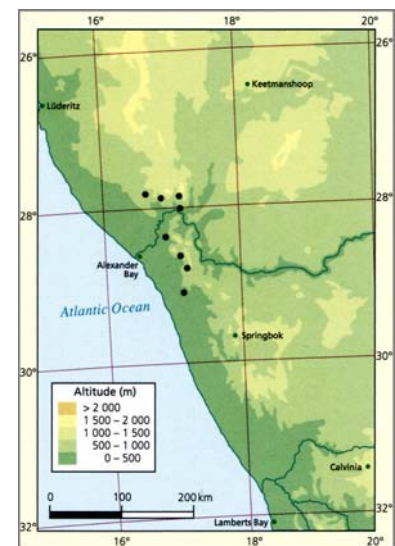


Fig. 17.43. Distribution of *Stapeliopsis neronis*.

STAPELIOPSIS NERONIS

lobes, outside of cylinder finely setose towards base, inside smooth with 5 longitudinal ridges joining towards base to dorsal surface of inner lobes; **inner lobes** 4.5-6.0 mm long, erect then connivent in upper half, laterally flattened, linear, tapering to slender terete obtuse apex, dorsally broadened towards base and for $\pm$ lower 1.5 mm fused to sides of outer corona tube.

Distribution and habitat

Stapeliopsis neronis is rare and known from relatively few collections. In Namibia it has been found in the mountains just north and east of Rosh Pinah and on some of the high slopes overlooking the Orange River, west of the mouth of the Fish River. In South Africa it is known from several scattered localities in the Richtersveld, where it has been recorded from north-west of Annisfontein and around Numees southwards to the Ploegberg and to as far south as Lekkersing and near Augrabies.

Stapeliopsis neronis occurs mainly on steep, south-facing quartzite, schist and gneiss slopes. These slopes are quite densely clothed with a typically highly succulent vegetation in which members of the succulent Aizoaceae and the

Crassulaceae form the dominant component. Plants grow under bushes, sometimes in quite dense vegetation or between rocks. These spots are often sufficiently steep that they experience little or no direct sunlight, especially during the winter.

Diagnostic features and relationships

Specimens of *S. neronis* can reach as large as 300 mm across. However, usually they are smaller, at around 150 mm in diameter, with the stems usually rather few and laxly clumping. The stems are unusually stout and are blue-green mottled with purple. This colouring is not only very attractive but it also enables them to blend in well with their surroundings. When exposed to the sun in habitat the stems become grey and very dull in appearance. The broadly deltoid but relatively small tubercles are joined into four conspicuously wing-like angles between which the stem is somewhat concave. A particularly unusual feature of the stems is that they are velvety to the touch, caused by a dense covering of fine papillae

(fig. 18 D, E). This allows mud splashed onto them by rain to remain there, adding to their inconspicuousness in habitat.

Flowers of *S. neronis* are not very large (usually around 25 mm long and at most 15 mm broad) but are the largest in the genus and must surely rank among the strangest in the family. The corolla is an almost perfectly ellipsoidal structure composed mainly of the corolla tube and with tiny lobes at the apex. The outside of both the tube and the lobes is deep purple with darker longitudinal veins and has a velvety appearance caused by a covering of small, acute papillae. On the interior the lobes and the mouth of the tube are white and the remainder is a similar purple to the outside. The lobes are erect and they surround a minute entrance to the tube that is less than 1.5 mm wide. This narrowing is brought about by considerable thickening of the corolla around the bases of the lobes, where the lobes are almost half as thick as they are broad. This makes them rigid and consequently they are unable to spread out more than to become erect. The inside is densely covered with papillae, which are quite tall in the upper half of the tube but fade away

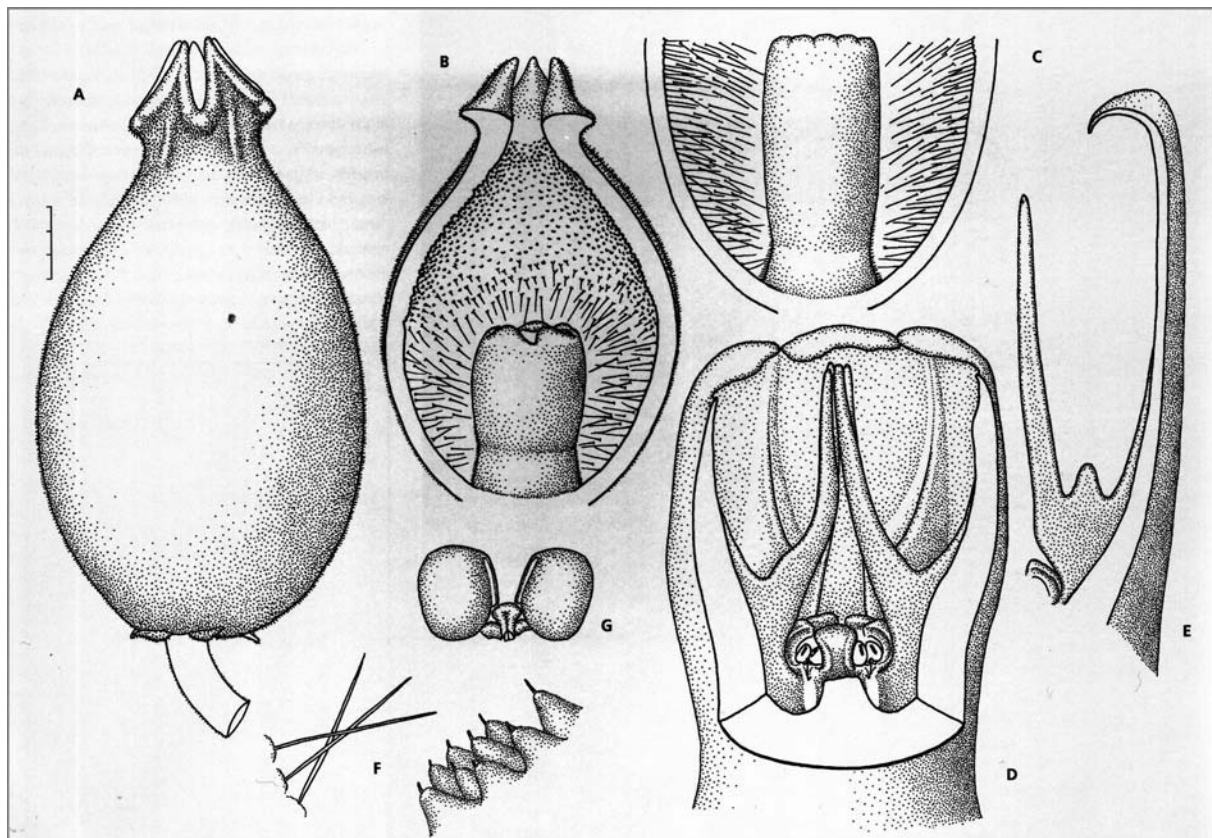


Fig. 17.44. *Stapeliopsis neronis*. A, side view of flower. B, C, side view of dissected flower. D, E, gynostegium with outer corona tube dissected. F, papillae inside corolla: those with long seta from base of tube; with short seta from just beneath mouth of tube. G, pollinarium. Scale bars: A-C, 3 mm (at A); D, E, 1 mm (at A); F, 0.5 mm (at A); G, 0.25 mm (at A). Drawn from: A, B, D, PVB 1385, just south of Lekkersing, Richtersveld; C, E, F, G, PVB 2818, Namuskluft, near Rosh Pinah, Namibia.

towards the base. Each papilla is tipped with a bristle and these are tiny in the upper half and become progressively longer towards the base, especially around the corona.

In *S. neronis* the outer corona consists of a cylindrical dark purple tube that is usually about twice as tall as broad, with five incurved, obtuse flaps at its mouth. On investigation, it was revealed that this structure develops by a combination of lateral and extreme vertical growth from five small meristems beneath the guide-rails (as is usually the case for the outer corona) and does not consist of parts contributed by the inner lobes. The inner corona lobes are rather frail and do not succeed in emerging from within this relatively massive outer corona, which therefore has to be dissected to see them. They are laterally flattened and slender, occasionally with a small, dorsal lobule and are fused, dorsally near the base, to the sides of the cylindrical outer corona.

Our studies (Bruyns *et al.* 2005) show that *S. neronis* is sister to a group consisting of *S. khamiesbergensis* and *S. urniflora* and that, within *Stapeliopsis*, the three of them form a very well supported northern group that is sister to the southern species.

History

Stapeliopsis neronis was discovered in October 1926 by the man called Nero, who drove the donkeys and the wagon with which N.S. Pillans entered the Richtersveld on that occasion. After this it remained very obscure and it was known in the living state to neither White & Sloane nor Carl Lückhoff. However, the collector and school-headmaster Pieter ('Piet') van Heerde (30 April 1893-14 May 1979) of Springbok (after whom *Namaquanthus vanheerdei* and *Vanheerdea* of the Aizoaceae, as well as many other taxa, were named) was acquainted with it, since he supplied flowers to the well-known German botanist Stefan Vogel just before 1954 (Vogel 1954). Material was discovered by Ernst FT. Rusch in the mountains near Rosh Pinah in southern Namibia sometime before 1964 (Huber 1967) and it was collected in this area again by W. Giess in 1974. Several further collections were made around 1972 (Lavranos 1975, Dyer 1978) in the southern part of the Richtersveld near Lekkersing, where it seems to have been first noticed by Helmut R. Tölken during his final researches into the Crassulaceae.

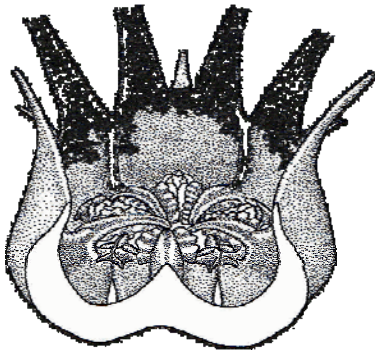


Fig. 17.45. *S. neronis*, PVB 1385, just south of Lekkersing, Richtersveld.



Fig. 17.46. *S. neronis*, PVB 5207, high ridges overlooking Orange River, Namibia.

18. Tavaresia



Tavaresia was established by Welwitsch in 1854 for plants that he had discovered along the coast of Angola near Luanda in December 1853. He named these plants *Tavaresia angolensis* and this new name was published in 1854 in the part of the *Boletim do Conselho Ultramarino* dealing with non-official matters. He dedicated the genus to Jose Tavares de Macedo, who was the assistant to the Minister

of Seas and Colonies in Lisbon. The reason for this dedication was that this ministry had assisted him in travelling to Angola to study plants there. He seems to have distributed material also under the name *Heurnia tavaresii* and this is mentioned in another publication which appeared shortly after the first, in *Annaes do Conselho Ultramarino* (Vol. 24: 252 (1856)) in which he described 71 *angolensis* again. Both of these descriptions of *T. angolensis* are very brief but can only refer to this species (Furtado 1967, Leach 1974b, 1993) and so the first of them constituted valid publication of *Tavaresia*.

Less than 20 years later Decaisne (1871) described the genus *Decabelone* for the same species, which he called *Decabelone elegans*.

In recent times there has been no doubt that the three species recognised by White & Sloane (1937) belonged to one genus. However, this genus has been known at different times in its history as *Tavaresia* or *Decabelone*, with Bullock (1957) and Brummitt (1992) making the most recent attempts to resurrect *Decabelone*. The matter of priority and validity of *Tavaresia* and the fact that this is the correct name for these plants was dealt with by Furtado (1967), Rozeira (1968) and twice by L.C. Leach (Leach 1974b, 1993).

Dyer (1954) described a further 'species', *T. meintjesii*. L.C. Leach (1974b) strongly suggested that this was a naturally occurring hybrid between a species of *Stapelia* and *T. barklyi* and this view was reinforced more recently by Alp (1989).

Much more recently another 'species', *T. thompsoniorum*, was described from a single specimen collected in southern Angola (Van Jaarsveld & Nagel 1999), this time with a very perfunctory description and some poor illustrations. In addition, no type specimen has been deposited. The authors described it as *T. thompsonii* but, as Jonkers (1999) pointed out, the name should have been '*thompsoniorum*', since it commemorated several members of the Thompson family. This plant has been collected also within Namibia and it is also suspected of being a hybrid (see 'Naturally occurring hybrids').

Although White & Sloane (1937) recognised three species, they were of the opinion that they were so closely related that one species was probably sufficient. Leach (1974b) reduced the number of species to two, namely *T. angolensis* and *T. barklyi*. These two species are readily separable on characters of the stems. In *T. angolensis* the stems are 6-8-angled and the two lateral spines on each tubercle are ascending relative to the stem, whereas in *T. barklyi* the stems are 10-14-angled (rarely 8-angled) and the lateral spines are descending. Only one of these, *T. barklyi*, occurs within southern Africa and is treated here.

Tavaresia Welw., *Bol. Cons. Ultr.*, parte nao official 7: 79 (1854).

Type: *Tavaresia angolensis* Welw.

Decabelone Decne., *Ann. Sci. Nat. Bot. Ser.* 5, 13: 404 (1871).

Type: *Decabelone elegans* Decne. [= *Tavaresia angolensis* Welw.].

The small genus *Tavaresia* is particularly distinctive with its spiky clumps of more or less cylindrical, 6-14-angled stems where each tubercle is tipped by three fine, sharp spines. This arrangement of spines is unique among the stapeliads.

White & Sloane (1937) placed *Tavaresia* after *Trichocaulon* and *Hoodia* in their account, so this might have been where they thought its affinities lay. At that stage these three genera contained the most 'cactus-like' of the stapeliads and most of them have cylindrical, many-angled stems where the leaves are modified into sharp spines. All the spiny stapeliads other than *Tavaresia* are now placed in *Hoodia* (Bruyns 1993). Although many of the characters of the stems (many angles, more or less smooth epidermis, similar surface of the spines, the occasional presence of small hairs at the bases of the spines) are common to *Hoodia* and *Tavaresia*, other characters indicate that

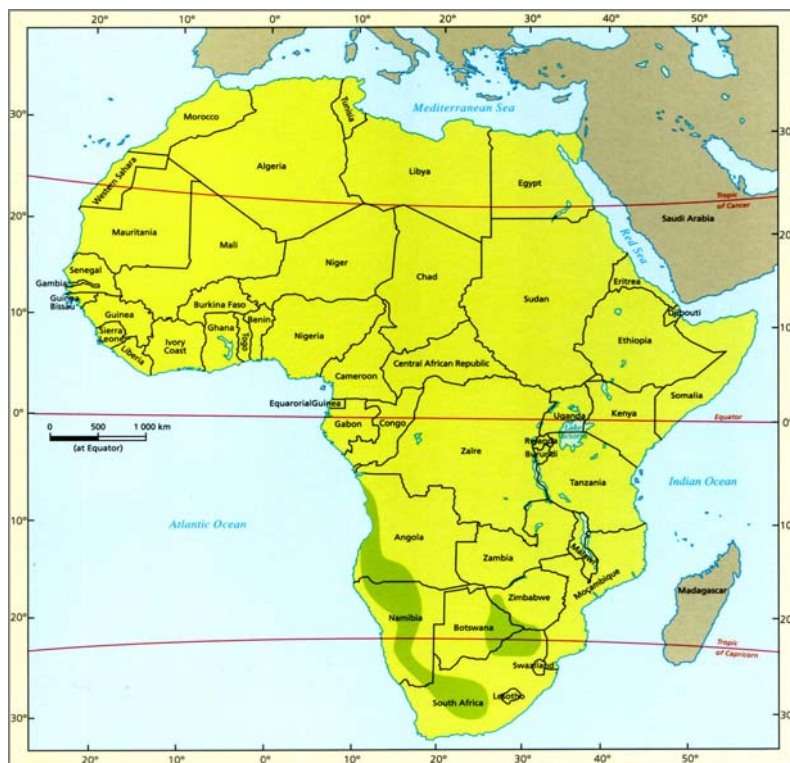


Fig. 18.1. Distribution of *Tavaresia*.

these two genera are not closely allied.

The solitary inflorescences which arise near the bases of the stems, the comparatively large, tubular flowers which are densely papillate all over the inside but have no annular thickening, the relatively long, slender sepals and large pollinaria suggest an affinity with *Huernia*. However, *Tavaresia* differs from *Huernia* in several details of the flower. The inner and outer coronal series are fused together at maturity and are not well separated. There is no obvious inner guide-rail. The style-head is concave rather than convex and, finally, the pollinarium lacks all the distinctive '*Huernia*' features (i.e., the short corpuscle, the shape of the caudicles, and the ellipsoidal pollinia with the insertion-crest exactly along the outer edge).

In all these characters *Tavaresia* and *Stapelianthus* share the same state. In particular, apart from the strange swellings at the tips of the outer corona lobules, the construction of the corona in *Tavaresia* and *Stapelianthus*

is extremely similar. In most species of *Stapelianthus* the outer lobes are usually a little more separated to near their bases but a more fused, cupular structure is found in *S. pilosus*. In *Stapelianthus* the style-head is also concave above. In most of them (*S. pilosus* excepted) the corpuscles are also secreted well above the anthers and the guide-rails slope outwards rather than vertically downwards, exactly as in *Tavaresia*. Although the stems in *Stapelianthus* are quite variable in their orientation and in the number of angles, those of *S. decaryi* show many similarities to stems of *Tavaresia* and in this species the flowers are also most similar to those of *Tavaresia*. In all species of *Stapelianthus* the epidermal cells of the stems have flat outer walls as in *Tavaresia*, though the stems are not bullate in *Tavaresia* as is often (though not always) the case in *Stapelianthus*. Consequently, *Tavaresia* shares the most morphological features with *Stapelianthus*.

Molecular data used by Meve & Liede

(2002) show only that *T. barklyi* is a member of an unresolved 'soft-stemmed' grouping. Our own molecular data have shown that it is closely associated with *Orbea*. However, when morphological data are included, it is closest to *Stapelianthus* (Bruyns & Klak 2004).

Tavaresia has a wide distribution in the arid to semi-arid parts of tropical and subtropical Africa south of the equator. *Tavaresia angolensis* is recorded from the coastal region of Angola from Ambriz, which lies north of Luanda, southwards to Namibe (Mocamedes) and is generally found within 60 km of the sea. It grows mostly in sandy areas on low outcrops of rock among dunes. *Tavaresia barklyi* is very widely distributed in southern Africa. The two species are not known to occur together anywhere.

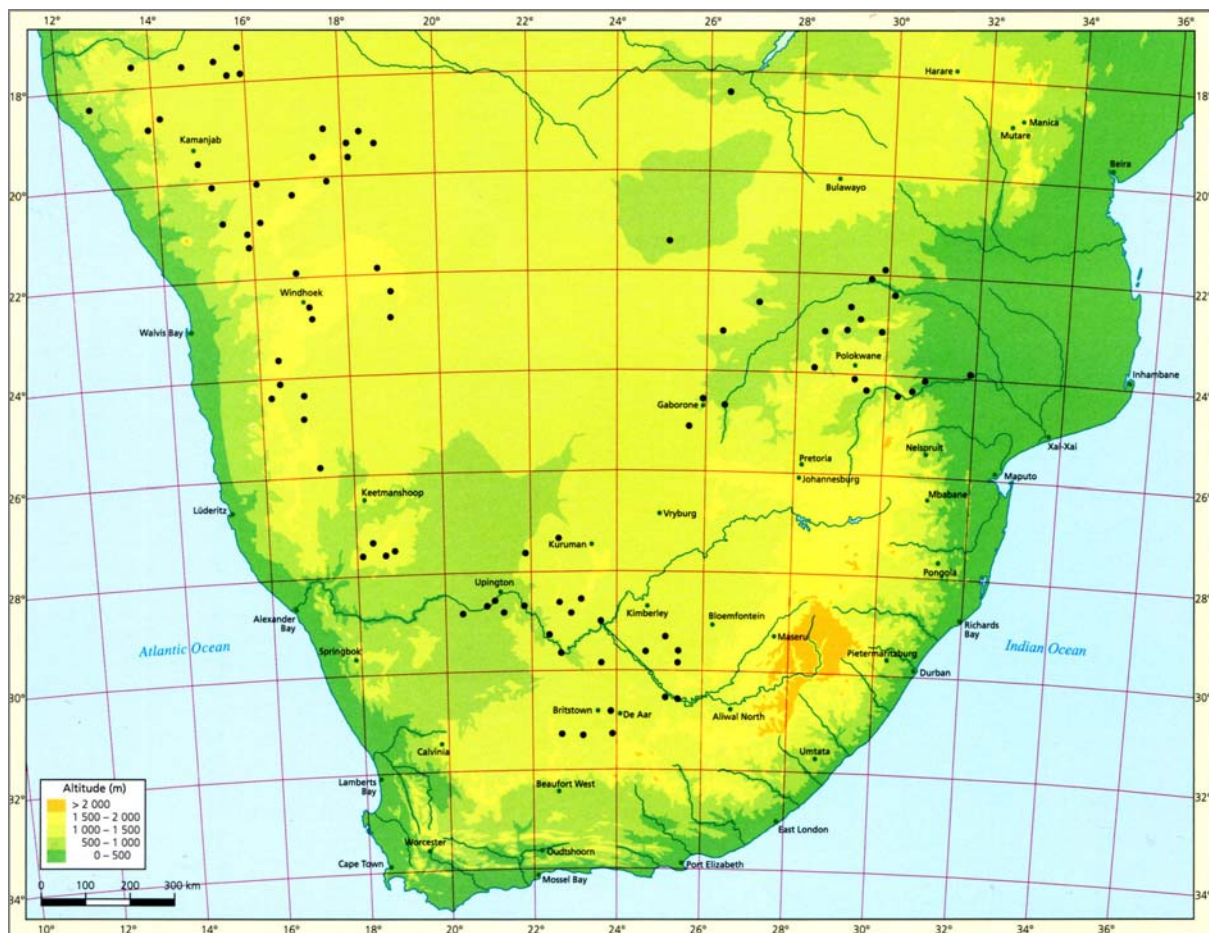


Fig. 18.2. Distribution of *Tavaresia barklyi* in southern Africa.

TAVARESIA BARKLYI

Tavaresia barklyi

Tavaresia barklyi (Thistleton-Dyer) N.E.Br., *Fl. Trop. Afr.* 4(1): 494 (1903).

Decabelone barklyi Thistleton-Dyer, *Bot. Mag.* 101: t. 6203 (1875).

Lectotype (designated here): South Africa, Cape, Du Plooy's Dam in the Karoo near the Orange River (near Prieska), collected 1871, *Barkly* 3/74 (K).

Euphorbia antunesii Pax, *Bot. Jahrb. Syst.* 34: 79 (1904).

Type: Angola, Huila, Antunes 72 (missing).

Decabelone grandiflora Dinter, *Deutsch-SWA: Flora, Forst u. landwirtschaftliche Fragmente*: 113 (1909).

Tavaresia grandiflora (Dinter) A.Berger, *Stap. u. Klein.*: 45 (1910).

Lectotype (designated here): Namibia, Arits, 19 Dec. 1908, *Dinter* 821 (SAM).

T. grandiflora var. *recta* Van Son in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1145 (1937).

Type: unknown.

Spiny succulent non-rhizomatous shrublet, branching at base to form dense clumps 50 mm-1 m diam. **Stems** 15-300 mm long, 10-25 mm thick, $\pm$ erect from very shortly decumbent base, fleshy and firm, glabrous, green to purplish; **tubercles** conical, laterally flattened and joined into (8-) 10-14 angles up stem, each tipped with 3 bristles (central bristle horizontal, laterals shorter and descending), without stipular denticles. **Inflorescence** glabrous, 1 per stem, with few flowers developing successively near base of young stems, nearly sessile, with several narrowly lanceolate bracts 3-8 mm long often with lateral teeth; **pedicel** 5-15 mm long, 1.5-2.0 mm thick, spreading; **sepals** 5-15 mm long, 1.5-2.5 mm broad at base, lan-

ceolate, acuminate, often spreading towards tips. **Corolla** 25-150 mm long, 20-80 mm diam., deeply tubular to funnel-shaped, usually initially ascending then spreading or curved downwards towards mouth, rarely straight, very shallowly lobed; outside glabrous, smooth to minutely & sparsely papillate, longitudinally flecked and barred with maroon on cream to greenish; inside densely covered with columnar to clavate papillae (increasing in length towards base of flower) each tipped with a short bristle, with round to longitudinally elongated maroon spots on pale yellow coalescing towards base into dark maroon patch around gynostegium; **tube** 25-150 mm long, widening gradually from base to 25-45 mm at mouth; **lobes** 12-25 mm long, 10-20 mm broad at base, deltate, spreading, shortly acuminate, slightly concave from somewhat upturned margins, margins eciliate. **Corona** 9-18 mm tall, 5-8 mm broad, consisting of 2 series of lobes arising on staminal tube and partly intergrown, seated on short broad and somewhat inflated pentagonal stipe streaked with maroon on white, lower fused parts white, upper filiform parts orange to irregularly striped with maroon on white; **outer lobes** fused towards base into tube $\pm$ half as high as broad, at mouth of this each lobe dividing into 2 erect dorsiventrally flattened filiform segments (often with a third small erect tooth between them) each of which is tipped with a spherical to tear-shaped pendulous knob; **inner lobes** $\pm$ 1.5 mm long, adpressed to backs of anthers and sometimes slightly longer than them, linear, dorsiventrally flattened, joined dorsally towards base to inside of outer corona cup, streaked with maroon on white. **Anthers** descending towards centre of style-head, margins not shrinking back but covering pollinia, $\pm$ semicircular. **Pollinium** D-shaped, longer than broad, insertion-crest twisting from outer edge onto dorsal surface, caudicle attached with broad cupular pad to base. **Follicles** erect, terete-fusiform, 60-150 mm long, 8-10 mm thick, obclavate, stout, diverging at about 30°, pale cream longitudinally striped with purple-brown, glabrous, smooth.

Distribution and habitat

Tavaresia barklyi has an enormous distribution over southern Africa, mainly in arid and semi-arid zones. It has been recorded from Angola (from Huila Province in the south), Namibia (where it is absent only from the north-east, the eastern parts and the south-western corner which receives rain in winter), South Africa (where it is mainly found in the arid centre of the country and in the extreme north along the valleys of the Limpopo and Olifants rivers), Botswana (where there are a few records around Gaborone and others northwards to Serowe and Orapa) and from Zimbabwe (in the west near Hwange and in the south around Beit Bridge along the Limpopo River).

This distribution shows many similarities to that of *Orbea lugardii*, except that *O. lugardii* is much more plentiful in the mixed sand and calcrete regions of south-eastern Namibia and western Botswana.

Tavaresia barklyi is usually found in stony locations. It is frequently to be seen on calcrete or limestone outcrops where it grows in crevices in the rocks or around the bases of spiny bushes or trees. Apart from its occurrence on some of the calcareous sands of western Ovamboland, it is not found in sandy areas. In fact, the presence of deep sand seems to be one of the factors affecting its distribution in Namibia, since areas covered with Kalahari sand are not, as a rule, inhabited by *T. barklyi*. Similarly, the distribution in Botswana may also be determined by the presence of sand over much of this country but the relative lack of records may also be due to insufficient collecting as it appears to be widely distributed along the eastern side of Botswana. Its known occurrence in Zimbabwe is also very scanty and this too may be due to insufficient collecting.

Diagnostic features and relationships

Plants of *T. barklyi* vary very much in size, from small clumps of stems no more than 60 mm across, with individual stems between 15 and 40 mm tall, to huge clumps up to and even over 1 m in diameter where the stems may reach 300 mm tall. The stems are mostly densely packed so the plant forms a relatively impenetrable, extremely spiny cluster, but this depends very much on the extent to which it is exposed and shaded plants can be quite laxly branched. The stems are cylindrical and erect and they have an unpleasant odour when cut. Along them the tubercles are closely arranged into 10-14 thin, continuous, wing-like angles. Each tubercle is tipped with a series of three very fine, spike-like bristles which together constitute a highly modified leaf-rudiment. One of the spines continues directly from the apex of the tubercle while the other two spread downwards from its base. Initially the whole leaf-rudiment is alive



Fig. 18.3. *T. barklyi*, PVB 4154, southern foot of Naukluft, Namibia, in habitat, March 1993, plant about 0.5 m in diameter.

but it soon dies, hardening into a spine which eventually wears off towards the base of the stem. These spines are sharp and needle-like if dry but become soft if moistened. Although the two lateral spines look rather like stipules, they are actually modifications of the lower margins of the leaf-rudiment (Meve & Albers 1990b) and the whole structure seems to be similar to the 'trifoliate' leaves found in other

asclepiads such as *Ceropegia paricyma* and *Microlooma sagittatum*.

The flowers are borne on small inflorescences near the bases of younger stems and, in healthy and strongly growing clumps, will sometimes be found all around the perimeter of the plant. Only a few flowers develop from each inflorescence and they do so in gradual succession. They remain open for two or three

days and emit a weak but unpleasant odour.

The flower in *Tavaresia* is a remarkable structure. It consists mainly of a tube between 25 and 150 mm long, which widens progressively from a narrow base to the mouth. At the mouth the relatively short lobes spread widely. The tube is sometimes straight but more usually arches up from the base and then descends slightly so as to touch the soil at the mouth. The

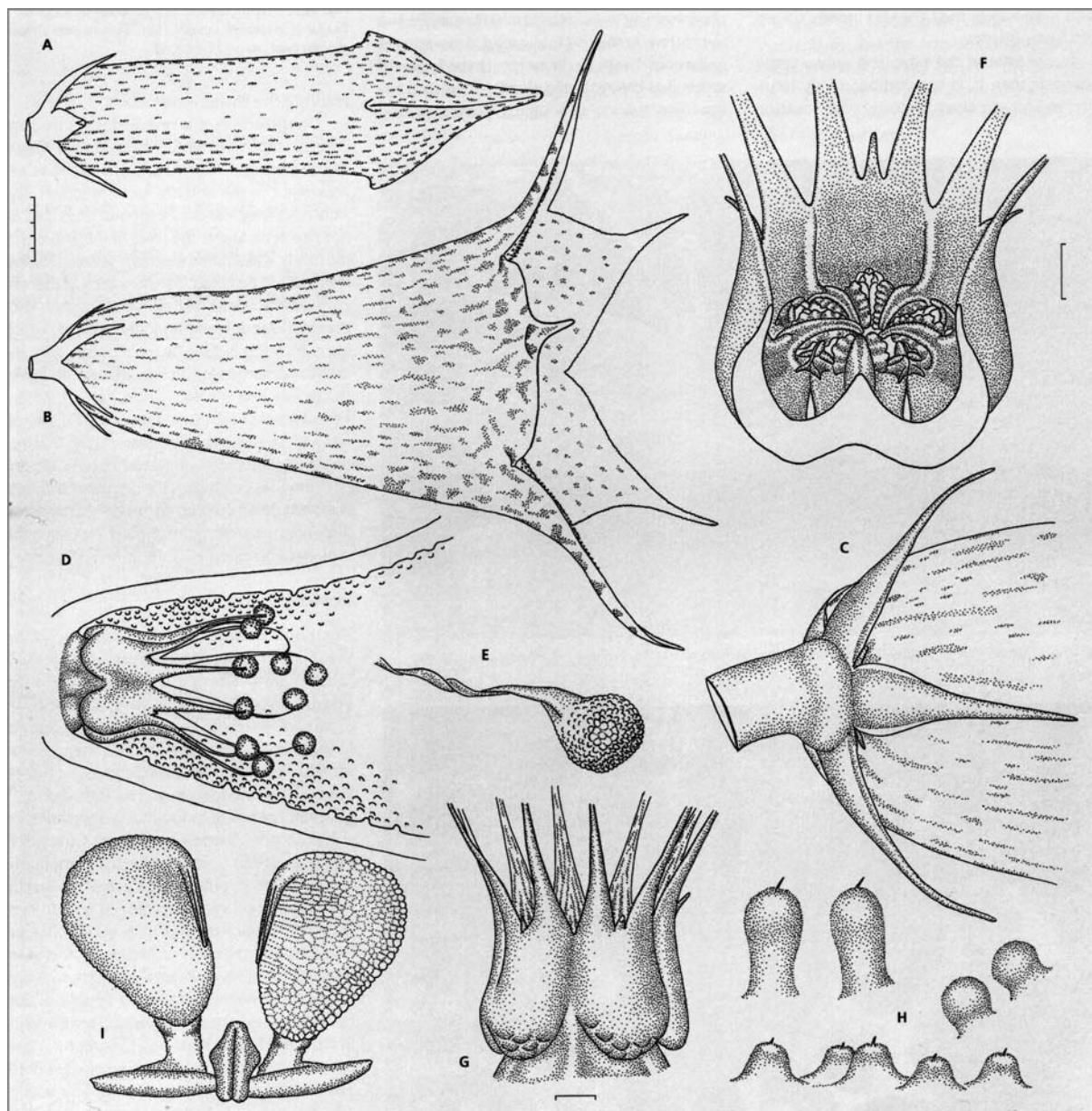


Fig. 18.4. *Tavaresia barklyi*. A, bud. B, side view of flower. C, calyx. D, side view of centre of dissected flower. E, ball on end of outer corona-lobule. F, gynostegium with outer corona-tube cut away showing broad mouths to guide rails and somewhat extended margins of the anthers. G, side view of gynostegium. H, papillae inside corolla: from base of tube (two groups above) and edge of lobes (group below). I, pollinarium. Scale bars: A-C, 5 mm (at A); D, 3 mm (at A); E, 1 mm (at A); F, 1 mm; G, 1 mm; H, 0.5 mm (at A); I, 0.25 mm (at A). Drawn from: A, B, D, F, G, H (upper right hand), I, Mullens 94, Victoria West; C, E, H (remainder), PVB 3492, eastern flank. Great Karas Mountains, Namibia.

TAVARESIA BARKLYI

whole of the exterior is always striped longitudinally with fine, broken maroon lines on a cream background and is mostly smooth but not shiny. The inside is a more intense cream with more widely spaced maroon markings. These take the form of spots on the lobes which elongate to short, longitudinal lines in the tube and they coalesce into a dark patch at the base of the tube. The inside is always covered with papillae, which are obscure on the lobes but increase slightly in length towards the base of the flower, where they are also usually tipped with a tiny bristle.

In the base of the tube, and only slightly narrower than it, is the comparatively large corona. This structure is mostly white outside

but it is streaked with maroon on the basal stipe, on the margins and inside of the outer lobes and on the inner lobes. The stipe is more or less as broad as the corona but in fact it is markedly inflated and inside, around the ovaries, it consists mainly of pockets of air. Above it, the five erect outer corona lobes are fused into a pentagonal tube. At the mouth of this tube each lobe is divided into two flat, slender lobules which are at least twice the length of the lower fused part. These lobules become progressively more slender and thread-like but then inflate at the end into a solid, drop-shaped ball about 1 mm in diameter. These balls are somewhat heavy for the slender threads bearing them and are pendulous, moving around



Fig. 18.5. *T. barklyi*, PVB 6555, Ga-Mankodi, south of Blouberg, in habitat, January 1996. Flowers with almost straight tube, about 10 cm long.



Fig. 18.6. *T. barklyi*, PVB 4154, southern foot of Naukluft, Namibia, in habitat, March 1993, flowers about 10 cm long.



Fig. 18.7. *T. barklyi*, PVB 4472, near Alldays, in habitat, January 1991, plant about 0.3 m in diameter.

readily if the flower is disturbed.

On dissection, it is revealed that this outer coronal cup considerably exceeds the height of the anthers. The inner corona lobes are adpressed to the anthers and are joined dorsally near their bases to the outer ones, but do not rise at all above the level of the anthers. If the inside is examined carefully, several unusual features will be noted. Between each anther the corpuscle is raised well above the anther, with the caudicles descending to the pollinia, which are completely hidden by the anthers. Also, the anthers descend slightly towards the centre of the flower and the very short guide-rails are almost horizontal, often with a widely gaping mouth. The peculiar arrangement of these organs is intimately connected with the unusually thin and conspicuously concave shape of the style-head, which also has particularly high points between the anthers on which the corpuscle is seated.

History

Tavaresia barklyi was first observed by the physician and naturalist Martin H.C. Lichtenstein. He saw it in July 1805 near Prieska on the Orange River, during an expedition from the Cape Colony to Kuruman in the north-eastern part of the colony. It also seems to have been gathered sometime before 1830 by J.F. Drege (Brown 1907-09), though I have not been able to locate any specimens of this collection. Subsequently another name, *T. grandiflora*, was described for the particularly large-flowered plants that generally occur in Namibia and were discovered by M. Kurt Dinter in 1898. Although it is generally true that these large-flowered plants are found in the tropics and over most of Namibia and that the small-flowered ones grow mainly in the Northern Cape from Griqualand southwards to De Aar, Victoria West and Colesberg, it has been found that occasional large-flowered ones occur in the Prieska district and small-flowered ones may be encountered in Namibia. White & Sloane (1937) already indicated that *T. grandiflora* and *T. barklyi* were difficult to separate and Leach (1974b) took a broad view, reducing *T. grandiflora* to synonymy.

19. Tridentea



Haworth (1812) named his genus *Tridentea* for the 'ligulae tridentiformis', a phrase that is generally assumed to refer to the tridentate outer corona lobes. He included in it a miscellany of five 'species': *T. gemmiflora*, *T. stygia*, *T. moschata*, *T. vetula* and *T. simsii*, the last two with some misgivings. *Tridentea stygia* and *T. moschata* are both synonyms of

gemmiflora. *T. vetula* and *T. simsii* are synonyms of *S. hirsuta* var. *vetula*, so it seems that Haworth considered *T. gemmiflora* to represent a 'typical *Tridentea*'. *Tridentea* was treated informally as a section of *Stapelia* by J.A. Schultes and by Stephan L. Endlicher (1836-40) and validly established as a section of *Stapelia* by Decaisne (1844), though with a few further species such as *S. paniculata* included.

Leach (1978b, 1980a) revived *Tridentea* and, taking *T. gemmiflora* as the type, placed in it a total of 17 species which had formerly belonged to *Caralluma* and *Stapelia*. In Bruyns (1995a) it was shown that several of these were more closely related to others in *Tromotriche* and as a consequence of this *Tridentea* was modified to include only the eight species of the sections *Tridentea* and *Parvipunctia* of Leach (1980a). Both Leach (1980a) and Bruyns (1995a) recognised two sections but these are abandoned here.

Meve & Liede (2002) used only *T. virescens* in their molecular survey of the stapeliads and found (e.g. in their fig. 4) that it was nested

within *Orbea* alongside *O. gerstneri* and *O. 'keithii'*. Our own investigations, in which three species (*T. marientalensis*, *T. peculiaris* and *T. virescens*) were used, found *Tridentea* to be a very well-supported monophyletic entity that is quite separate from *Orbea*. The position that their '*T. virescens*' occupied was taken up in our analysis by *Orbea lugardii*, a common and widespread species that is vegetatively very easily mistaken for a *Tridentea*. Since no voucher existed for their '*T. virescens*' (Meve & Liede 2002, Liede, pers. comm. 2004), it is highly likely that the odd position of their '*T. virescens*' was simply due to misidentified material. Our results, however, have not resolved the relationships of *Tridentea* to the other stapeliad genera.

Tridentea Haw., Syn. PL Succ., 34 (1812).

Stapelia [unranked] *Tridentea* Schult. in Roem. & Schult., Syst. Veg. 6: 31 (1820).

Stapelia sect. *Tridentea* (Haw.) Decne in DC, Prodr. 8: 656 (1844).

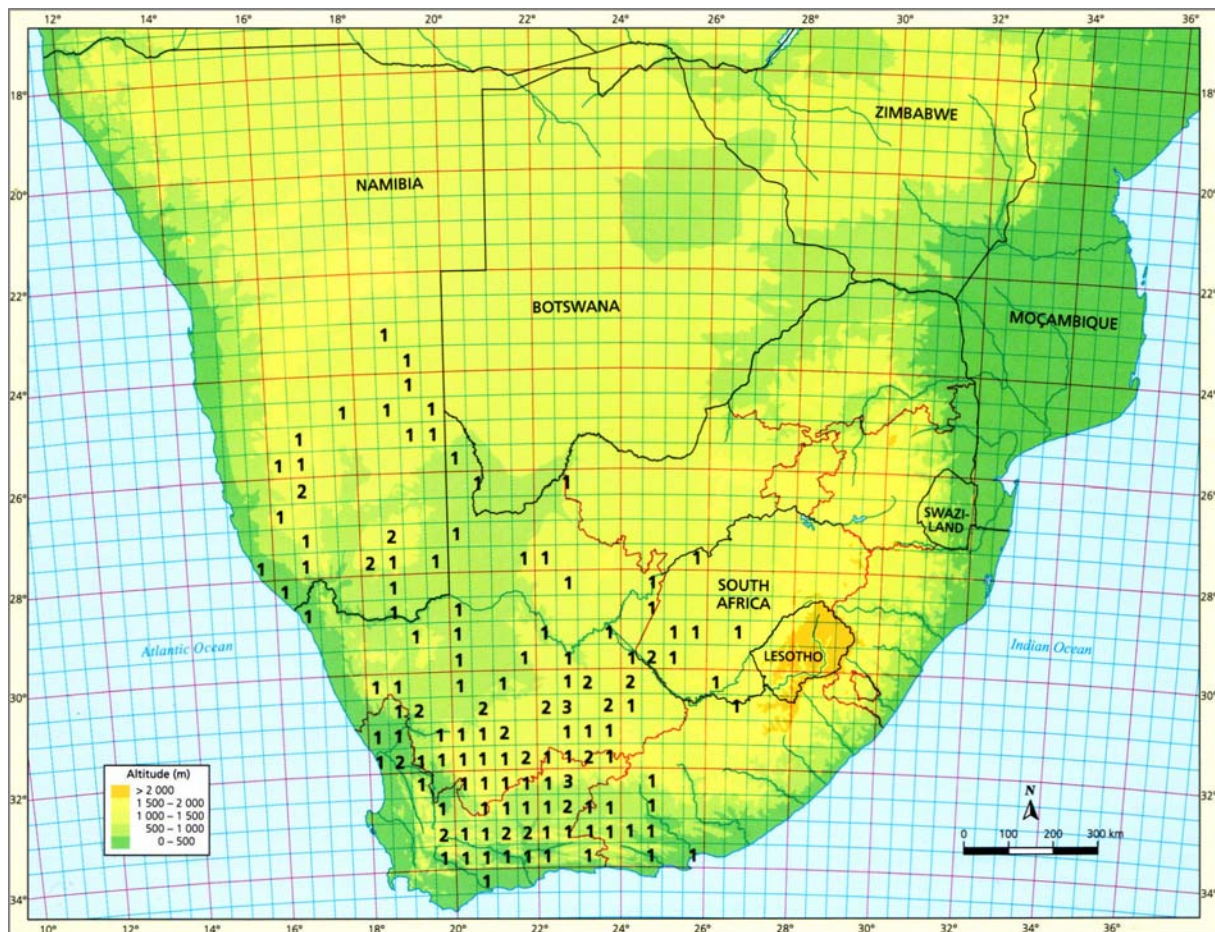


Fig. 19.1. Patterns of diversity in *Tridentea*, showing the number of species recorded to date in each half-degree square.

TRIDENTEA

Lectotype: *Tridentea gemmiflora* (Masson) Haw.
Tridentea sect. *Parvipunctia* L.C.Leach, *Excelsa*
Taxon. Ser. 2: 5 (1980).

Type: *Tridentea parvipuncta* (N.E.Br.) L.C.Leach.

Small spineless rarely slightly rhizomatous succulent forming compact clump 30-500 mm (-1 m) diam. **Stems** 30-150 (-200) mm long, 8-20 (-25) mm thick, decumbent, fleshy and soft, glabrous, pale green to greyish green often flecked with brown; **tubercles** 2-3 mm long, rectangular in outline, submammary, laterally slightly flattened and joined in lower half into 4 (-6) very obtuse (rounded) angles along stem; each bearing a widely spreading fleshy deltoid to subulate caducous **leaf-rudiment** 1.5-10.0 mm long (leaving a whitish scar) subtended by a patch of minute hairs on either side sometimes extending along margin, without stipular denticles. **Inflorescence** glabrous, 1 per stem, arising near base of stem, bearing 1-5 flowers developing in gradual succession on stout gradually lengthening peduncle 5-20 (-40) mm long with several lanceolate bracts 1-2 mm long without lateral teeth; **pedicel** 25-80 mm long, $\pm$ 2 mm thick, spreading to ascending; **sepals** 4-6 mm long, 2.5-3.0 mm broad at base, lanceolate, acute, sometimes with few marginal cilia. **Corolla** 20-100 mm diam., rotate to campanulate, usually lobed to about half of radius or less; outside glabrous and smooth; inside smooth to slightly rugose or papillate (papillae usually each with apical bristle); **tube** shallowly to deeply conical, with corolla often much thickened around mouth but not raised into annulus; **lobes** 8-35 mm long, 6-30 mm broad at base, spreading to recurved, ovate-deltate, acute, slightly convex, margins usually with vibratile cilia. **Corona** 3-10 mm tall, 4-15 mm broad, consisting of 2 series arising on staminal tube and slightly intergrown only near bases, glabrous, raised on short stout pentagonal stipe; **outer lobes** 1-8 mm long, ascending to spreading, simple to trifid, dorsiventrally flattened and channelled down middle, laterally fused only near base with bases of inner lobes; **inner lobes** 1-10 mm long, adpressed to backs of anthers, usually much exceeding them and rising in centre of style-head in small column, dorsiventrally flattened at least towards base (often terete above), often with laterally flattened $\pm$ deltoid dorsal horn in lower half. **Anthers** horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** D-shaped, longer than broad, insertion-crest twisting from outer edge onto dorsal surface, caudicle attached with broad cupular pad to base. **Follicles** erect, terete-fusiform, obclavate, slender to stout, with horns diverging at 30-60°, longitudinally mottled with broken narrow purple stripes, glabrous, smooth.

Plants of *Tridentea* form dense clumps which may reach anything up to 1 m in diameter, though they are mostly much smaller and, in the Great Karoo, they are often only 50-80 mm across. The stems, which are of markedly similar appearance and size throughout the genus, are always erect from a short horizontal base. Only occasionally do they exhibit a slightly rhizomatous habit, as in *T. peculiaris* and more rarely in *T. dwequensis*. They have a remarkable ability to shrivel in severe drought and in this state become flaccid so that the whole plant collapses into a soft heap which rapidly recovers

when rain falls. In several species the roots are unusually thick (up to 5 mm in diameter) and these probably also assist in storing moisture to ensure the plant's survival.

Here the tubercles on the stems are only slightly laterally flattened and are joined vertically into four rows. Adjacent tubercles are pressed somewhat against one another so that between the angles there is only a narrow groove. Each tubercle bears a leaf-rudiment, which is situated not in the middle of the tubercle (relative to the axis of the stem) but close to the base of the next tubercle above. These leaf-rudiments may reach 10 mm long in *T. gemmiflora*, *T. marientalensis* and *T. virescens* and are then quite obvious, though remaining slender. In the remaining species they mostly do not exceed 3 mm long but are quite conspicuous on new growth, except in *T. pachyrrhiza*. They are usually spreading, often nearly as thick as broad and then with a slight constriction at the base. Around the base they always have a cluster of multicellular, often somewhat phallic hairs (with cylindrical stem and swollen apex) which sometimes extend along the margin of the leaf as well (fig. 19 E, F).

The surface of the stems and of the leaf-rudiments is smooth and somewhat shiny. One of their remarkable characteristics is that, when turgid, they are edible and have a pleasant, lettuce-like flavour and consistency.

Flowers develop near the bases of the stems and appear in gradual succession on a peduncle which may eventually lengthen to 100 mm. All parts of the inflorescence are glabrous.

Flowers vary in *Tridentea* between 20 and 100 mm across and are mostly rotate with a shallow, bowl-shaped depression in the centre. Only in *T. dwequensis* does a significant tube develop and there the flower is campanulate. In *T. virescens* the corolla is deeply lobed but in the others (except *T. dwequensis*) the lobes are broad and relatively short, and are fused into a flat area outside the tube. In all except *T. dwequensis* the corolla is thickened around the gynostegium and this somewhat accentuates the steepness of the sides of the tube. This thickening is mostly only visible when the flower is dissected. The one exception to this is *T. peculiaris*, where there is a more obvious swelling around the mouth of the tube. In this case dissection reveals that the corolla tube is entirely formed by this thickening in an otherwise flat flower. Flowers in *Tridentea* are usually brightly coloured and very beautiful but extremely evil-smelling. All except *T. virescens*, where the flowers are uniformly yellow or greenish, are mottled with yellowish to greenish spots on a brown to purple background.

The outside of the flower is wholly smooth but the inside is almost always papillate and covered, usually very densely, with multicellular, cylindrical to pyramidal papillae whose apical cell is usually extended into a bristle. In

T. gemmiflora and even more so in *T. virescens* (but to a lesser degree in *T. dwequensis*) these papillae become fused into transverse, almost tooth-like ridges in which the summits of individual papillae can still be distinguished. The margins of the lobes almost always have some vibratile, clavate cilia along them.

In *Tridentea* the gynostegium is raised on a stipe but this is generally short, only just lifting the corona above the base of the tube. Two series of corona lobes are present and, as in *Stapelia*, the two series can easily be distinguished, although they are not significantly vertically separated on the staminal tube. The outer lobes are always somewhat channelled above. In several species each lobe has two lateral processes (present only as flaps in *T. dwequensis* but as distinct lobules in several others) but these are entirely absent in *T. jucunda* and *T. parvipuncta*. The inner lobes are always dorsiventrally flattened, adpressed to the backs of the anthers and exhibit the variation found in many genera: short and about as long as the anthers (*T. parvipuncta*, *T. peculiaris*) to rising in the centre in a column (*T. jucunda*) which is especially long and slender in *T. dwequensis*. They are often ornamented with a laterally flattened, fin-like horn.

The pollinaria are D-shaped (markedly narrow in *T. gemmiflora*, *T. marientalensis* and *T. pachyrrhiza*) with especially short caudicles and short, almost square corpuscles.

The eight species of *Tridentea* are widely distributed over the western and southern half of southern Africa in southern Namibia, South Africa and the south-western corner of Botswana. In South Africa they are found over most of the drier western parts, becoming more scattered in the drier western parts of the Free State.

Most of the species occur over wide areas and slight peaks in concentration (up to three per half-degree square) occur where these areas overlap. Two localised taxa are found within the winter-rainfall parts of Namaqualand. *Tridentea pachyrrhiza* occurs in the Namib Desert around the mouth of the Orange River at Alexander Bay on the border between Namibia and South Africa. The other localised species is *T. peculiaris*, which inhabits the lower parts of the Sout and Olifants rivers near Vanrhynsdorp. The Orange River did not always enter the sea at Alexander Bay and, at one stage, it drained into the Atlantic near the present-day mouth of the Olifants River (Dingle & Hendey 1984), so it is around the former outlet of the Orange River that this second localised species of *Tridentea* occurs. Both of these species inhabit sandy places and this is also often the case for *T. marientalensis* along the south-eastern edge of the Kalahari.

Key to the species

1. Outer corona lobes trifid 2.
2. Inner corona lobes each with distinct dorsal horn, lobes adpressed to backs of anthers but much exceeding anthers and recurved above, dorsal horns distinctly laterally flattened, corolla with no trace of annulus in centre 3.
3. Corolla inside uniformly bright yellow to greenish yellow, 20–30 mm diam., lobes usually without marginal cilia 5. *T. virescens*
3. Corolla inside with maroon, brown or purple-black mottling on cream to pale yellow (or pale mottling on dark), 40–100 mm diam., lobes with marginal cilia 4.
4. Corolla lobes with margins folding upwards, pedicels mostly < 50 mm long, papillae on corolla ± without apical bristle 5.
5. Lateral teeth of outer corona lobes at least half as long as central tooth, leaf-rudiments 5–10 mm long 6. *T. gemmiflora*
5. Lateral teeth of outer corona lobes less than half as long as central tooth, leaf-rudiments 1–2 mm long 7. *T. pachyrrhiza*
4. Corolla lobes with margins not folding upwards, pedicels mostly > 70 mm long, papillae on corolla each tipped with a long bristle 8. *T. marientalensis*
2. Inner corona lobes with no dorsal horn, lobes adpressed to backs of anthers but not rising above them in centre, corolla often with distinct annulus in centre 4. *T. peculiaris*
1. Outer corona lobes bifid or simple 6.
6. Inner corona lobes adpressed to backs of anthers but much exceeding anthers to rise in narrow column in centre 7.
7. Corolla campanulate, covered inside with obtuse conical papillae, outer corona lobes linear-lanceolate with broad ascending lateral flaps at base 3. *T. dwequensis*
7. Corolla usually rotate, ± smooth inside, outer corona lobes without broad lateral flaps near base 1. *T. jucunda*
6. Inner corona lobes adpressed to backs of anthers but not rising above them in centre 2. *T. parvipuncta*

1. *Tridentea jucunda*

Tridentea jucunda (N.E.Br.) L.C.Leach, Trans. Rhod. Scient. Assoc. 59: 3 (1978).

Stapelia jucunda N.E.Br., Fl. Cap. 4 (1): 975 (1909).

Lectotype: South Africa, Cape, near Douglas, *E. Pillans* sub N.S. Pillans 644 (BOL).

Stapelia jucunda var. *deficiens* N.E.Br., Fl. Cap. 4 (1): 976 (1909).

Type: Victoria West district, Biesiespoort, N.S. Pillans 675 (BOL).

Stapelia cincta Marloth, Trans. Roy. Soc. South Africa. 3: 125 (1913).

Tridentea jucunda var. *cincta* (Marloth) L.C.Leach, *Excelsa Taxon. Ser.* 2: 33 (1980).

Type: Cape, Nuweveld Mountains near Beaufort West, Marloth 5116 (PRE).

Stapelia dinteri A.Berger in Dinter, *Neue Pflanzen Deutsch-SWAs*: 51 (1914).

Tridentea jucunda var. *dinteri* (A.Berger) L.C.Leach, *Excelsa Taxon. Ser.* 2: 34 (1980).

Type: Namibia, Klein Karas, *J. Dinter* sub *Dinter* 3247 (SAM).2

Stapelia ausana Dinter & A.Berger ex Dinter, *Feddes Repert. Spec. Nov. Regni Veg.* 23: 365 (1927).

Lectotype (selected here): Namibia, Aus, *Dinter* 1144 (SAM).

Small succulent 60–150 mm diam. **Stems** 30–120 mm long, 8–15 mm thick; **leaf-rudiments** 1.5–5.0 mm long, subulate. **Inflorescence** with few flowers developing in rapid to gradual succession on spreading to erect peduncle 5–20 mm long; **pedicels** 15–30 mm long, 1–2 mm thick, erect to spreading; **sepals** 2.5–4.0 mm long, 1.7–2.0 mm broad at base, narrowly deltate to ovate, acute to acuminate. **Corolla** 20–35 mm diam., rotate to slightly cupular or conical; outside pale green, marked sometimes heavily with dark purple; inside cream with purple-brown to red-brown spots which become larger and more crowded

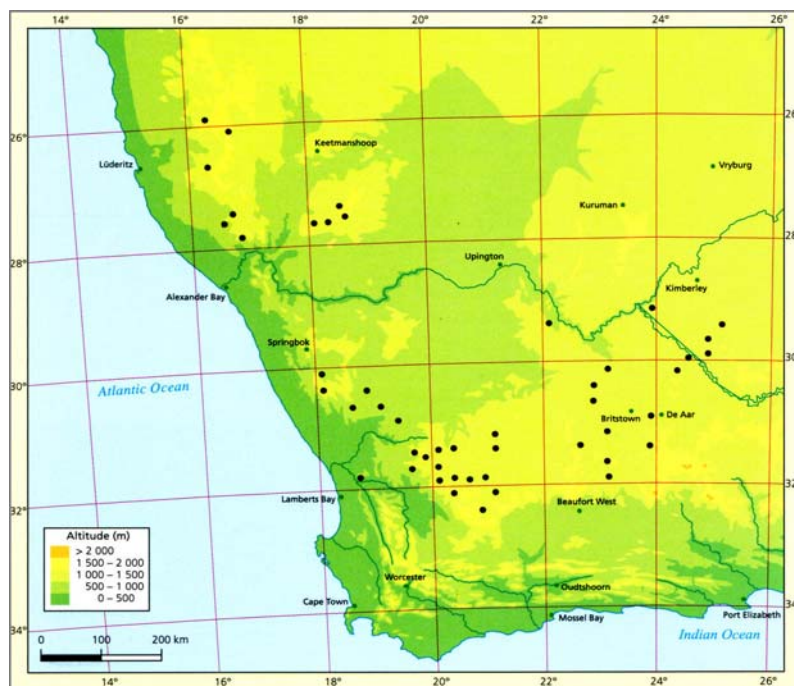


Fig. 19.2. Distribution of *Tridentea jucunda*.

towards margins and apex and merge to form continuous dark border, sometimes faintly rugulose or with low dome-shaped papillae each with minute apical bristle; **tube** 1–2 mm deep, cupular, with corolla much thickened around mouth (below bases of lobes); **lobes** 6–10 mm long, 6–10 mm broad at base, spreading to recurved, ovate to deltate-ovate, acute, sometimes with marginal cilia. **Corona** ± 5–7 mm tall, 5–7 mm broad, raised on short stipe; **outer lobes**

± 2.5–3.0 mm long, 1 mm broad, ascending, narrowly deltoid, acute to broadly obtuse to shortly to deeply bifid (lobules diverging), slightly channelled on inner surface, purple-brown; **inner lobes** 3–5 mm long, connivent then ascending in narrow column and often recurved towards apices, terete and ± filiform above anthers, obtuse, sometimes with small dorsal gibbosity to laterally flattened horn near base, cream marked with purple.

TRIDENTEA JUCUNDA

Distribution and habitat

Tridentea jucunda is found over a wide area in southern Namibia and western South Africa. In Namibia it grows in the south-west between Aus and Witpütz and around the Great Karas Mountains further east. In South Africa it occurs along the eastern flanks of the Kamiesberg southwards to around Sutherland and Fraserburg in the Great Karoo and eastwards to Kimberley and the western corner of the Free State.

Diagnostic features and relationships

Over this vast area, *T. jucunda* is extremely variable. Leach (1980a) recognised three varieties but Meve (1988a) pointed out that these were extremely difficult to recognise in practice. In Bruyns (1995a) further evidence was presented and it was shown that this should all be considered as a single widespread species without any varieties or subspecies.

Flowers are always spotted with purple-



Fig. 19.3. *T. jucunda*, PVB 6272, south-east of Sutherland.

brown (sometimes somewhat reddish) on cream but quite often these spots coalesce into a dark border along the edges of the lobes. This border is particularly often present in collections from southern Namibia and also especially in the area between Loeriesfontein, Sutherland and Fraserburg, where plants that possessed it were at one stage known as *Stapelia cincta*. This dark border is usually (but not always) absent from collections further north-east towards Kimberley and the Free

State, where the flowers are mostly uniformly spotted right to their edges.

In *T. jucunda* the flowers sometimes have a few papillae inside, particularly in the small corolla tube, but they are mostly entirely smooth. There are sometimes cilia along the margins of the lobes.

The outer corona lobes are channelled above but tend to become narrower towards the apex. As in *T. parvipuncta*, they lack any kind of lateral lobules. The inner lobes rise in the centre into a slender column of variable length and may have a small, flattened, dorsal fin towards the base.

History

N.E. Brown described *Stapelia jucunda* from two specimens, both of which came from the area near Douglas. The first to have been gathered was found by Mary Elizabeth Barber, probably between 1869 and 1886, when she lived with her husband on the 'diamond fields' near Kimberley. The other was collected by Eustace Pillans in 1906.

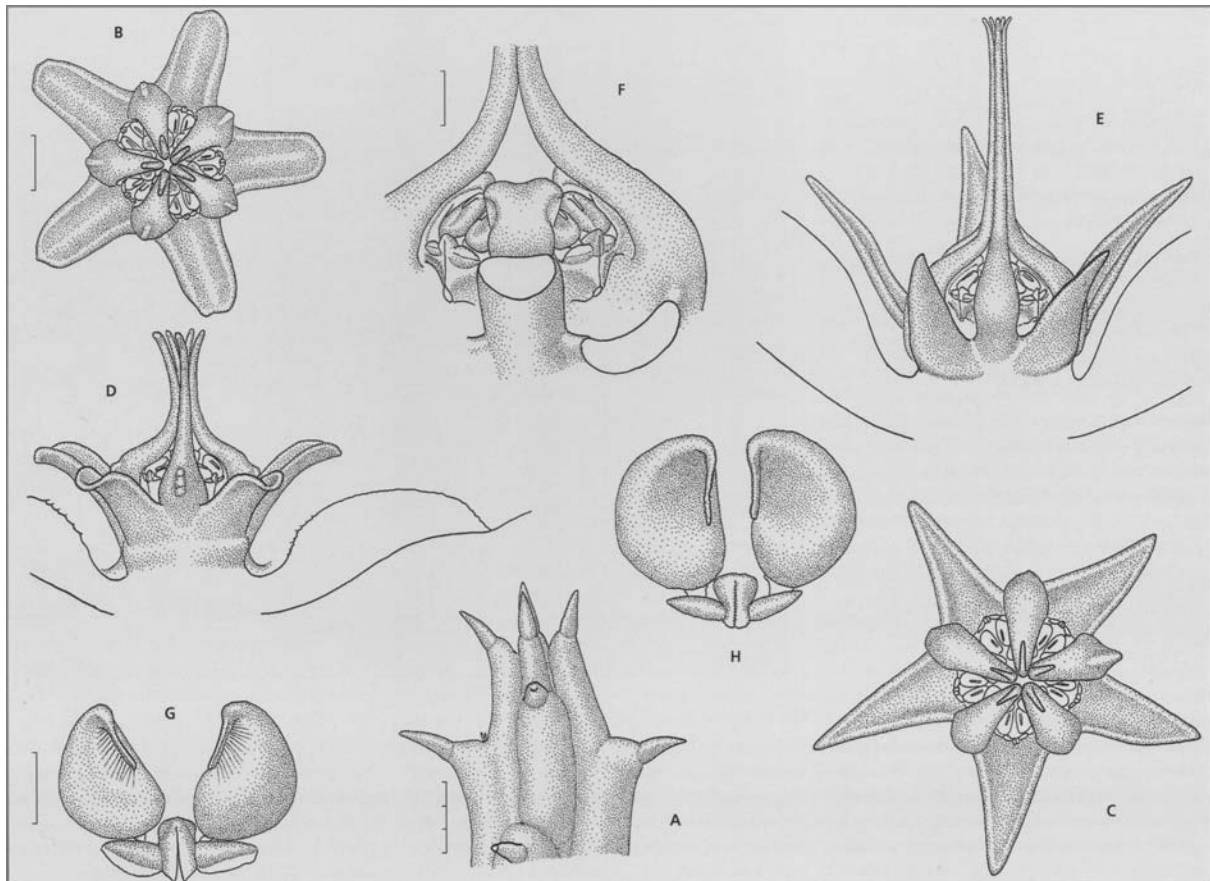


Fig. 19.4. *Tridentea jucunda*. A, apex of stem. B, C, face view of gynostegium. D, E, side view of centre of dissected flower. F, gynostegium with 2 outer and one inner corona lobe excised. G, H, pollinarium. Scale bars: A, 3 mm; B-E, 1 mm (at B); F, 0.5 mm; G-H, 0.25 mm (at G). Drawn from: A, B, D, G, PVB 3318, south of Prieska; C, E, F, H, PVB 3908, Sebrafontein, near Rosh Pinah, Namibia.

TRIDENTEA PARVIPUNCTA



Fig. 19.5. *T. jucunda*, PVB 5119, west of Petrusville.



Fig. 19.6. *T. jucunda*, PVB 5332, east of Paulshoek, Kamiesberg.



Fig. 19.7. *T. jucunda*, PVB 7961, east of Loeriesfontein.



Fig. 19.8. *T. jucunda*, PVB 3742, south of De Aar.

2. *Tridentea parvipuncta*

Tridentea parvipuncta (N.E.Br.) L.C.Leach, Trans. Rhod. Scient. Assoc. 59: 3 (1978).
Stapelia parvipuncta N.E.Br., Hooker's Icon. Pl. 20: t. 1923 (1890) [as '*S. parvipunctata*', K.Schum. in Engl. & Prantl, *Pflanzenfam.* 4 (2): 278 (1895)].
Type: South Africa, Cape, Nuwveld Mountains, Bain, comm. Barkly (K).

Small succulent 60-150 mm diam. **Stems** 30-120 mm long, 8-15 mm thick; **leaf-rudiments** 2-3 (-5) mm long, subulate. **Inflorescence** with few flowers developing in rapid to gradual succession on spreading peduncle up to 20 mm long; **pedicels** 20-60 mm long, 2-3 mm thick, spreading with upturned apex so that flowers often $\pm$ humifuse; **sepals** 2-3 mm long, 1.25 mm broad at base, narrowly deltoid, acute. **Corolla** 22-35 mm diam., rotate (rarely campanulate); outside pale dull green spotted with purple-brown and obscurely 5-nerved on each lobe; inside pale cream to greenish finely spotted with purple-brown (spots becoming slightly larger towards margins and there sometimes coalescing into narrow purple-brown border), faintly rugulose but not papillate; **tube** a very shallow ($\pm$ 1 mm deep, occasionally somewhat deeper in subsp. *truncata*) depression in centre of flower, corolla slightly thickened around mouth (towards bases of lobes); **lobes** 8-10 mm long, 10-12 mm broad at base, spreading with recurved apices, ovate to ovate-deltate, acute, sometimes with simple to slightly clavate cilia. **Corona** 2.5-3.0 mm tall, 4.0-6.5 mm broad, raised on short stipe; **outer lobes** 1-3 mm long, 1.0-1.5 mm broad, ascending then spreading, shiny black, deeply bifid into obtuse $\pm$ terete diverging lobules to $\pm$ rectangular and truncate-emarginate; **inner lobes** $\pm$ 1 mm long, shorter than to exceeding anthers and meeting in centre but not rising above anthers, yellow with black margin all round, narrowly deltoid, $\pm$ acute, near base sometimes with small dorsal gibbosity.

Tridentea parvipuncta is found in the Great Karoo south of Beaufort West and in the Ceres Karoo. An isolated record cited by Leach (1980a) from Douglas is considered here to be doubtful and is not included among the records.

Vegetatively this species cannot be distinguished from either *T. jucunda* or *T. dwequensis*.

Flowers in *T. parvipuncta* are similar to those of *T. jucunda* and in both species the corolla is relatively small and flat, and spotted with purple-brown on cream to greenish. These

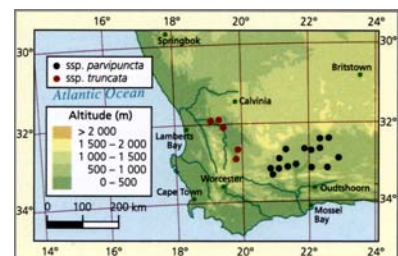


Fig. 19.9. Distribution of *Tridentea parvipuncta*.

TRIDENTEA PARVIPUNCTA

spots are often, but not always, much finer in *T. parvipuncta* than in *T. jucunda*. The inside of the corolla is faintly and irregularly rugose but is generally without papillae.

In *T. parvipuncta* the corona more or less fits into the shallow tube, with the outer lobes spreading out towards the surface and the inner adpressed to the anthers. It is easily separated from that of *T. dwequensis* and *T. jucunda* by the fact that these inner lobes are short and do not rise at all above the anthers in a central column. Typical also for *T. parvipuncta* is the fact that the outer corona lobes become broader towards their tips rather than narrower. These lobes provide an easy way to separate the two subspecies that are recognised: the apex is produced into two obtuse, almost cylindrical, diverging lobules in subsp. *parvipuncta* whereas it is truncate and somewhat apically notched in subsp. *truncata*.

2a. *Tridentea parvipuncta* subsp. *parvipuncta*

Corolla lobes usually with marginal cilia. **Outer corona lobes** usually deeply bifid into obtuse diverging lobules.

Distribution and habitat

Subsp. *parvipuncta* is more or less confined to the relatively low-lying, south-western corner of the Great Karoo from Matjiesfontein to Beaufort West and southwards to Prince Albert, Klaarstroom and Rietbron.

Plants grow in flat areas at the base of hills in firm, sometimes gravelly ground. They may be found sheltering under plants of a gregarious, spiny species of *Ruschia* or other shrublets or under larger bushes of *Lycium*.

Diagnostic features and relationships

In subsp. *parvipuncta* the flowers are often borne on long, slender pedicels which lie on the ground and have the flower facing upwards at the apex. The corolla is always extremely finely spotted with purple-brown on cream, sometimes with a slight, dark border near the margins.

History

Subsp. *parvipuncta* was first collected in the Nuweveld Mountains near Beaufort West by Thomas C. Bain and sent to N.E. Brown at Kew by Henry Barkly before 1877.

Key to the subspecies of *T. parvipuncta*

- Outer corona lobes deeply bifid into obtuse diverging lobules 2a. subsp. *parvipuncta*
Outer corona lobes ± truncate, emarginate 2b. subsp. *truncata*

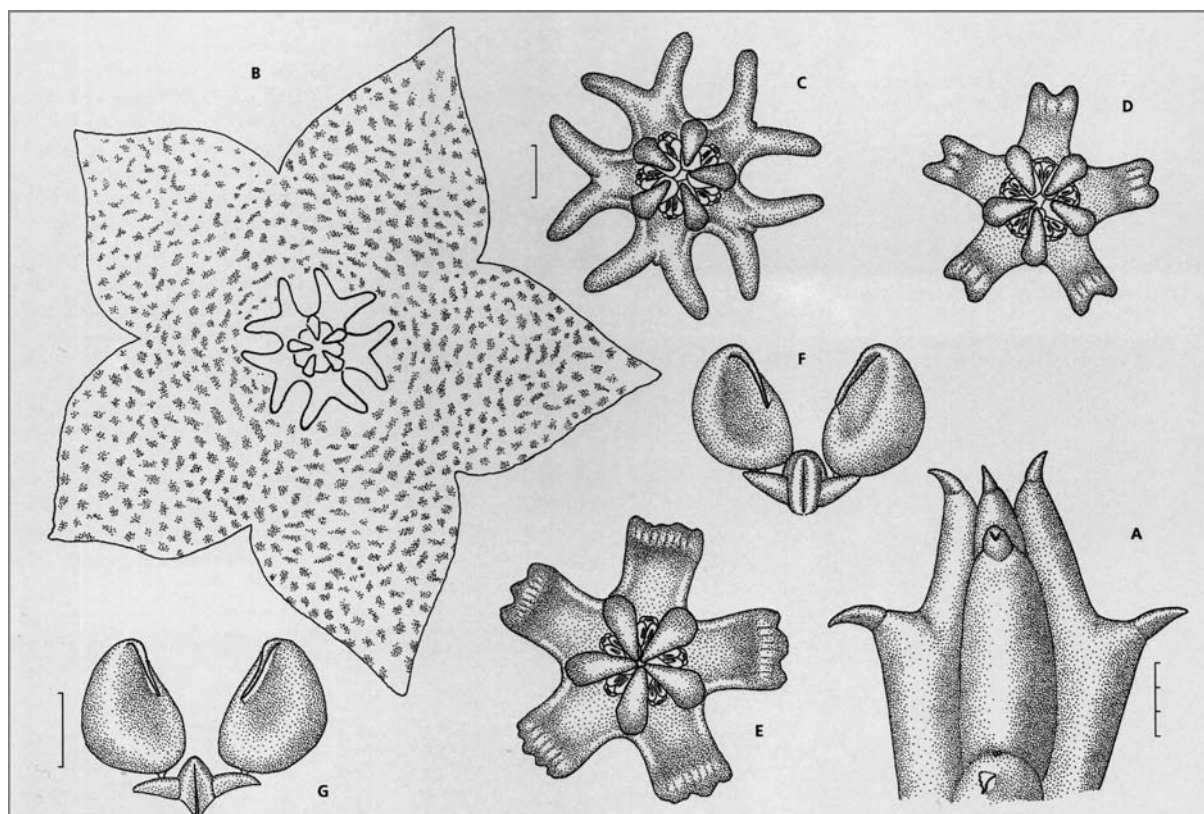


Fig. 19.10. *Tridentea parvipuncta* (A-C, F, subsp. *parvipuncta*; D, E, G, subsp. *truncata*). A, apex of stem. B, face view of flower. C-E, face view of gynostegium. F, G, pollinarium. Scale bars: A, B, 3 mm (at A); C-E, 1 mm (at C); F, G, 0.25 mm (at G). Drawn from: A, PVB 3246, Prutkraal, west of Rietbron; B, C, F, PVB 3284, Moordenaarskaro, north of Laingsburg; D, E, G, PVB 4274, 48 km north of Karooport, Ceres Karoo.

2b. *Tridentea parvipuncta* subsp. *truncata*

T. parvipuncta subsp. *truncata* (C.A.Lückh.)

Bruyns, S. *African J. Bot.* 61 :194 (1995).

Stapelia parvipuncta var. *truncata* C.A.Lückh. in A.C.

White & B. Sloane, *Stap.*, ed. 2, 3:1145 (1937).

Tridentea parvipuncta var. *truncata* (C.A.Lückh.)

L.C.Leach, *Excelsa Taxon. Ser.* 2: 31 (1980).

Type: South Africa, Cape, Ceres Karoo, Dwequa River, J. Lückhoff (missing).

Neotype: Cape, Botterkloof, Hall sub NBG 229/56 (NBG).

Tridentea pusilla Frandsen, *Aloe* 29: 40 (1992).

Type: Cape, Botterkloof, Frandsen FR5 (PRE).

Corolla lobes without marginal cilia. **Outer corona lobes** $\pm$ truncate, emarginate.

Distribution and habitat

Subsp. *truncata* is found on the western side of the Ceres Karoo from north of Karooport along the foot of the Swaruggens north-westwards to Botterkloof and in some of the dry valleys of the northern and north-eastern parts of the Cedarberg.



Fig. 19.12. *T. parvipuncta* subsp. *parvipuncta*, PVB 3284, Moordenaarskaro, north of Laingsburg.



Fig. 19.13. *T. parvipuncta* subsp. *parvipuncta*, PVB 3990, south of Beaufort West.



Fig. 19.14. *T. parvipuncta* subsp. *parvipuncta*, PVB 3246, Prutkraal, west of Rietbron.



Fig. 19.11. *T. parvipuncta* subsp. *truncata*, PVB 4274, 48 km north of Karooport, Ceres Karoo.

Diagnostic features and relationships

The corollas in subsp. *truncata* and subsp. *parvipuncta* are very similar in colour and shape, with the main difference being found in the lack of marginal cilia in subsp. *truncata* which are mostly present in subsp. *parvipuncta*. The pedicels are often much shorter in subsp. *truncata* but this difference is not reliable. The distinctions in the respective coronas are outlined above.

It is not at all clear why *T. pusilla* was described. On careful examination of the descriptions of Leach (1980a) for *T. parvipuncta* var. *truncata* and Frandsen (1992) for *T. pusilla*, one finds that there is remarkable agreement between the two and they only differ in the smaller dimensions of the pedicel, corolla and

gynostegium. However, these are all features that are so variable in this genus that for the most part Leach (1980a) did not even attempt to provide bounds within which they could be expected to vary. In addition, notably smaller flowers are often produced in this genus (and others) towards the end of the flowering period or if the plant is either unhealthy or not properly established. Small flowers have been seen on plants of subsp. *truncata* from several localities, even in the Ceres Karoo, and there is therefore no justification for maintaining *T. pusilla* as a distinct species.

History

Subsp. *truncata* was discovered by James Lückhoff and his family along the Dwequa River in the Ceres Karoo in 1931.



Fig. 19.15. *T. parvipuncta* subsp. *parvipuncta*, PVB 8197, north of Klaarstroom. In this plant the outer corona lobes are short and rather similar to those of subsp. *truncata*.

TRIDENTEA DWEQUENSIS

3. *Tridentea dwequensis*

Tridentea dwequensis (C.A.Lückh.) L.C.Leach,
Exceisa *Taxon*. Ser. 2: 35 (1980).

Stapelia dwequensis C.A.Lückh. in A.C. White &
B. Sloane, *Stap.*, ed. 2, 2: 511 (1937).

Type: South Africa, Ceres distr., Dwequa River,
J. Lückhoff (missing).

Neotype: Pofadder, Hardy 738 (PRE).

Small succulent 60-150 mm diam. **Stems** 30-120 mm long, 8-15 mm thick; **leaf-rudiments** 1.5-2.5 mm long. **Inflorescence** with few flowers developing in rapid to gradual succession on spreading to erect peduncle 5-20 mm long; **pedicels** 20-30 mm long, 2 mm thick, ascending then spreading to hold flower facing outwards or slightly nodding; **sepals** $\pm$ 4 mm long, 1.5 mm broad at base, ovate, acute. **Corolla** 25-35 mm diam., campanulate; outside pale green irregularly mottled towards base with purple-brown; inside pale yellow or cream with deep

purple-brown spots becoming smaller in tube, covered with obtuse conical papillae each tipped with an apical bristle up to 0.5 mm long; **tube** 9-14 mm long, bowl-shaped, often somewhat pentagonal, with corolla only slightly thickened towards mouth; **lobes** 7-11 mm long, 8-12 mm broad at base, spreading and slightly recurved, ovate to ovate-deltate, acute, convex above, with few cilia up to 1 mm long along margins towards bases. **Corona** $\pm$ 10 mm tall, 9-10 mm broad, purple-black except for few yellow patches near bases of inner lobes, raised on very short stipe; **outer lobes** 5.0-6.5 (-8) mm long, 1.5-3.0 mm broad at base, ascending, margin conspicuously folded up to form pouch towards base, above narrowly attenuate and channelled on inner surface, acute; **inner lobes** 8-10 mm long, $\pm$ 1.25 mm wide at ovate base, connivent then ascending in slender narrow column $\pm$ equalling tube, terete and filiform above anthers with minutely obtuse or sometimes minutely clavate apices, without dorsal gibbosity.

Distribution and habitat

At the time of publication of White & Sloane in 1937, *T. dwequensis* was known only from the single collection of James Lückhoff. However, with time records have gradually accumulated and my own exploration has shown that it occurs over a wide area, with all its records coming from well to the east of the winter-rainfall region. Plants have now been gathered from the districts of Pofadder, Brandvlei, Williston, Camarvon and Fraserburg.

The area where *T. dwequensis* occurs is a dry, topographically and geologically rather uniform and monotonous part of southern Africa. Much of it is flat, punctuated by scattered shale hillocks and mountains or by occasional small doleritic dykes. Most of the larger shale hills are topped with a crust of dolerite. *Tridentea dwequensis* occurs mainly in flat areas

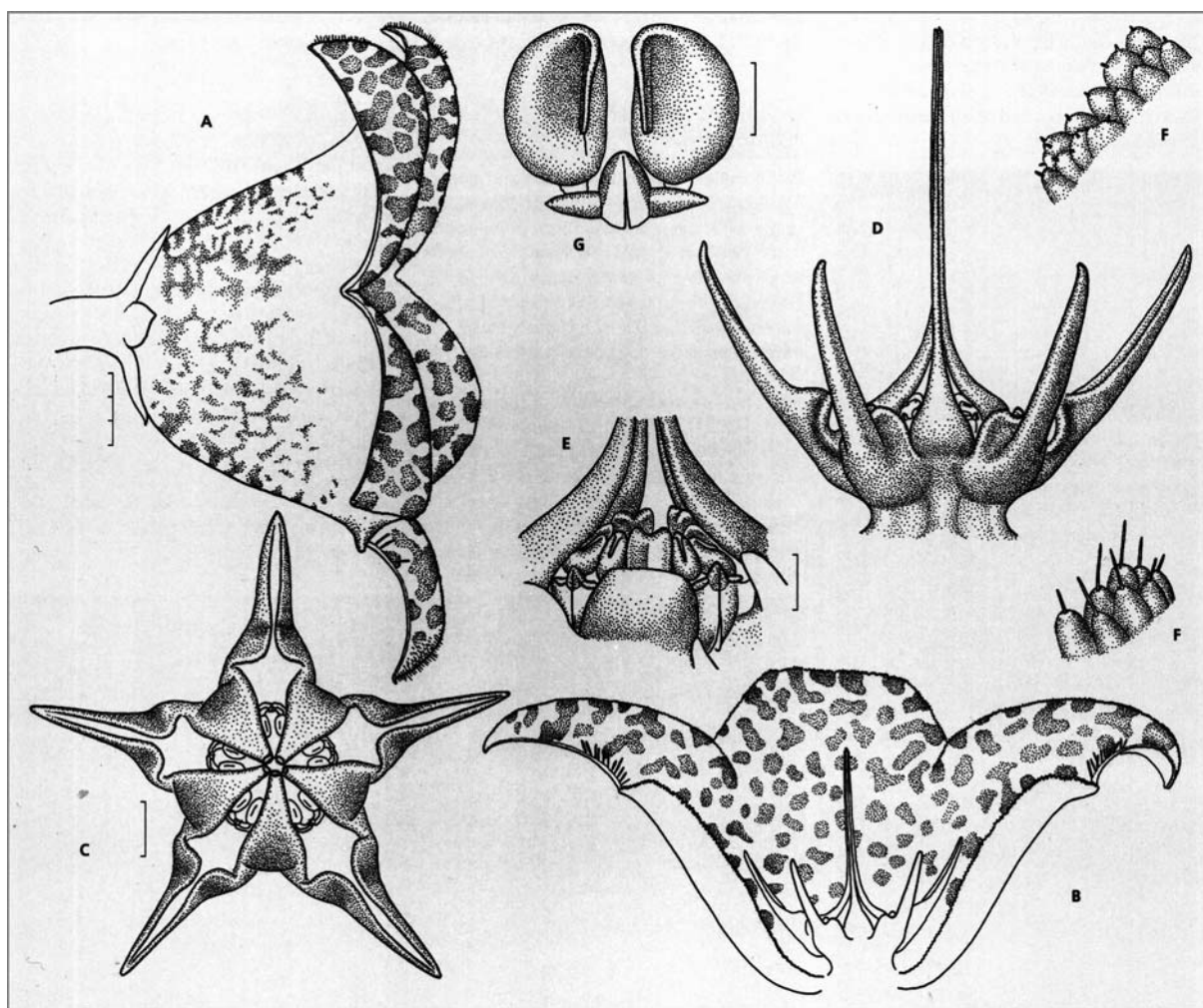


Fig. 19.16. *Tridentea dwequensis*. A, side view of flower. B, side view of dissected flower. C, face view of gynostegium. D, side view of gynostegium. E, centre of gynostegium with outer corona lobes and one inner lobe removed. F, papillae inside corolla: upper ones from mouth of tube, lower from near tips of lobes. G, pollinarium. Scale bars: A-B, 3 mm (at A); C-D, 1 mm (at C); E-F, 0.5 mm (at E); G, 0.25 mm. Drawn from PVB 3320, Williston.



Fig. 19.17. *T. dwequensis*, M. Scot, north of Williston.



Fig. 19.18. *T. dwequensis*, PVB 4872, north of Fraserburg.



Fig. 19.19. *T. dwequensis*, PVB 7544, north of Williston.

or on gentle slopes on shales or occasionally on calcretes. The vegetation over this area is very scanty and *T. dwequensis* will be found under shrublets of various kinds, such as *Rhigozum trichotomum* or *Ruschia spinosa*.

Although I have not actually found the two species growing together, the distributions of *T. dwequensis* and *T. jucunda* overlap and they have been found, especially around Williston, within a few kilometers of one another.

Diagnostic features and relationships

The plant of *T. dwequensis* is indistinguishable from that of *T. jucunda* both in the size of the stems, their colouring and the size and shape of the leaf-rudiments. However, in cultivation, the stems have been found sometimes to exhibit a slightly rhizomatous tendency which is absent in *T. jucunda*.

The flowers of *T. dwequensis* are held on an ascending and then spreading pedicel so that they usually have a slightly nodding habit. They are campanulate with quite a deep, bowl-shaped corolla tube in which there is no sign of any annular thickening, although the base of the tube is slightly thinner than it is higher up and it may also be distinctly pentagonal towards the base. Around the mouth of the tube there are fairly short lobes which spread strongly. Inside, the corolla is particularly strikingly coloured, with bold and fairly large,

deep purple-brown spots on a pale yellow or cream background. Towards the edges of the lobes these spots tend to coalesce, while lower down in the tube they also often coalesce into irregular, roughly concentric rings. The flower gives off an unpleasant odour. The inside of the flower is covered, especially towards the tips of the lobes, with conical and obtuse papillae. Towards the tips of the lobes these are discrete but in the mouth of the corolla tube they sometimes become fused together into ridges, as in *T. virescens*. Each of these papillae has an apical bristle, which is quite long towards the tips of the lobes but becomes very short towards the mouth of the tube. The corolla lobes usually have a few small cilia along the margins near the base.

In this species the corona is just contained within the corolla tube. The outer lobes are much longer than those in *T. jucunda*. They are deeply channelled by the margins being folded upwards, and they are more or less adpressed to the sides of the corolla tube. Towards the base they abruptly become broader (though not as markedly as in species such as *T. gemmiflora* and *T. virescens*) and here on either side there is

a broad flap which is folded upwards to enclose a fairly deep cupular area beneath the guide-rails. The inner corona lobes are exceptionally long and slender from a broad, flattened base. In the centre they are pressed together and rise in a thin column which reaches as high as the mouth of the tube. They are much longer than in *T. jucunda* and, as far as is known, are always without a dorsal horn.

History

Tridentea dwequensis was described from material which was said to have been collected by James Lückhoff somewhere along the Dwequa River in 1931. This is one of the tributaries of the Doring River in the southern part of the Ceres Karoo and he seems to have discovered *T. parvipuncta* subsp. *truncata* in the same area. However, it has not been re-collected anywhere near here and it is possible that this locality is erroneous.

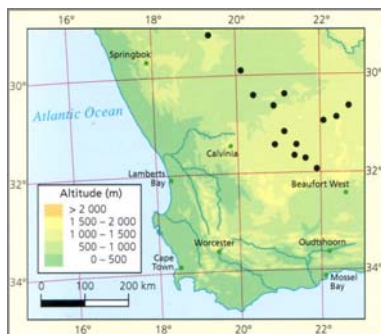


Fig. 19.20. Distribution of *Tridentea dwequensis*.



Fig. 19.21. *T. dwequensis*, PVB 4882, south-east of Williston.

4. *Tridentea peculiaris*

Tridentea peculiaris (C.A.Luckh.) L.C.Leach, *Trans. Rhod. Scient. Assoc.* 59: 4 (1978).

Stapelia peculiaris C.A.Luckh., 'S. A. G.' 29: 94 (1938).

Type: South Africa, Vanrhynsdorp division, Spuitdrif, P.L. Meiring sub Lückhoff 280 (BOL).

Small succulent 60-300 mm diam., sometimes with some stems spreading beneath the ground then emerging to form new clump. **Stems** 30-120 mm long, 8-15 (-20) mm thick; **leaf-rudiments** 1-3 mm long, $\pm$ deltoid. **Inflorescence** with few flowers developing in rapid to gradual succession on spreading peduncle up to 20 mm long; **pedicel** 20-25 mm long, 2 mm thick, ascending and holding flower facing partly upwards; **sepals** $\pm$ 3 mm long, ovate, acute. **Corolla** $\pm$ 30-10 mm diam., rotate; outside pale green to suffused with brown, with 3-5 longitudinal veins on lobes; inside yellow to green or reddish brown mottled irregularly (sometimes obscurely) with brown to dull purple or red and becoming paler towards centre, with low dome-shaped papillae joined into obscure and irregularly reticulated ridges, each papilla tipped with a minute bristle; **tube** $\pm$ 2 mm deep, nearly as broad as corona, shallowly cupular, formed by annular thickening of corolla near its base; **lobes** 9.0-12.5 mm long, 10-14 mm broad at base, spreading, ovate-deltate, acute to shortly acuminate, slightly convex above from margins slightly recurved especially towards base, with vibratile clavate purple cilia 1.5-3.0 mm long. **Corona** $\pm$ 3 mm tall, 7 mm broad, reddish brown, raised on short stipe; **outer lobes** $\pm$ 2 mm long, $\pm$ 2 mm broad at base, ascending then spreading parallel to surface of corolla, trifid; central lobule $\pm$ 1.5 mm long, narrowly deltoid, acute to obtuse or notched at apex, channelled on inner surface; lateral lobules $\pm$ deltoid, diverging, 0.5-1.0 mm long; **inner lobes** $\pm$ 1.5 mm long, shorter than to exceeding anthers and meeting in centre but not rising above anthers, narrowly deltoid to ovate, acute to obtuse, near base with small obtuse dorsal gibbosity or hornlet < 0.5 mm long.

Distribution and habitat

Tridentea peculiaris is associated with the Sout, Doring, Hol and the lower Olifants Rivers, where it is found from Koekenaap in the west to the foot of the Langeberg (north-west of Loeriesfontein) in the north-east and to Klawer in the south-east. The unusual red sands in this area appear to be relicts from the earlier drainage system of the Orange River through this region (see above) and *T. peculiaris* is endemic to these sands.

Plants of *T. peculiaris* do not grow in loose, wind-blown sand but are found where the sand has settled to become firm and very slightly loamy. Here they usually grow among colonies of various gregarious species of *Ruschia* (especially *R. comptonii* and *R. subsphaerica*) and *Zygophyllum*.

Diagnostic features and relationships

Tridentea peculiaris often exhibits a rhizomatous habit, to an extent that is unusual for *Tridentea*, though it is not as pronounced as, for example, in *Tromotriche revoluta*. Apart from this the plants are typical for the genus, with the usual soft, edible stems bearing small, subulate leaf-rudiments on the youngest tissue.

Flowers are produced on short pedicels around the bases of the stems and usually face at least partly upwards. The corolla is remarkable for its unusual combination of colours, with a background colour of anything from yellow to green or even reddish brown on which there is a dense, reticulated mottling of brown to red. It is generally flat to slightly reflexed and has broad, deltate lobes below which there is a united, more or less flat area. Dissection reveals

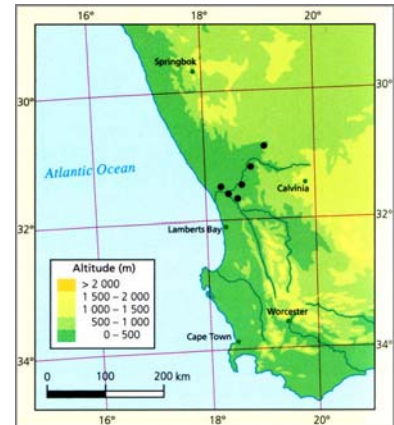


Fig. 19.22. Distribution of *Tridentea peculiaris*.

that towards the centre the corolla becomes distinctly thickened and this is the only species of *Tridentea* where there is any trace of a raised annulus around the gynostegium. This annulus is entirely responsible for the formation of the corolla tube for, on the underneath, the corolla is almost completely flat.

In the centre the reddish brown corona fits neatly into the tube formed by the annulus and does not project from it. The somewhat spreading outer lobes follow more or less the curvature of the mouth of the tube, though they are not pressed to it. In *T. peculiaris* the outer corona lobes are identical in shape to those of *T. virescens*. However, the inner lobes are quite small and have only a slight dorsal gibbosity.

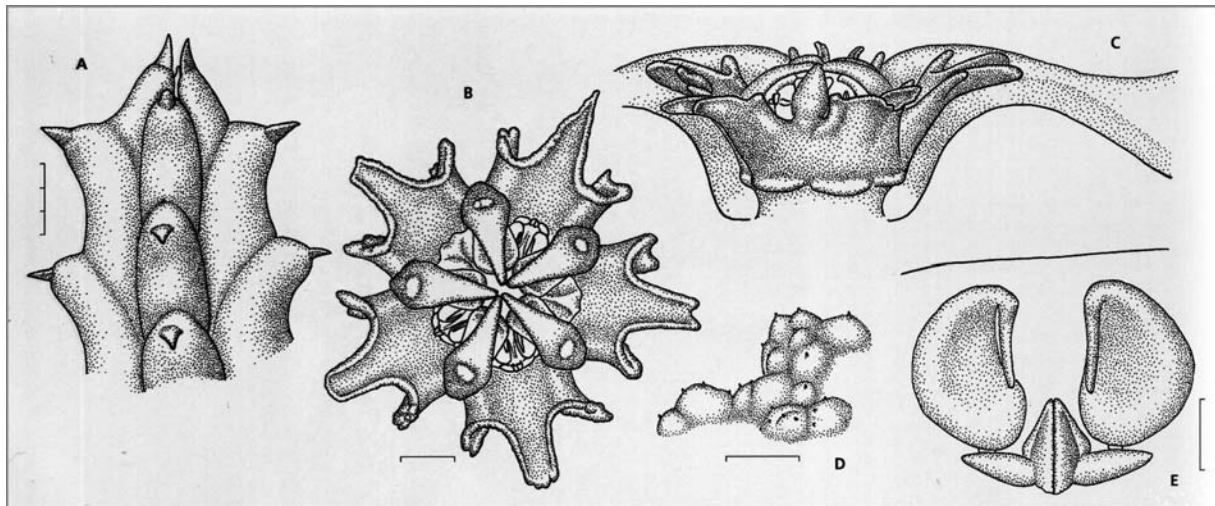


Fig. 19.23. *Tridentea peculiaris*. A, apex of stem. B, face view of gynostegium. C, side view of centre of dissected flower. D, papillae inside corolla towards tips of lobes. E, pollinarium. Scale bars: A, 3 mm; B, 1 mm (at B); D, 0.5 mm; E, 0.25 mm. Drawn from Nagel 65, Sout River Bridge, north of Vanrhynsdorp.



Fig. 19.24. *T. peculiaris*, Quaggaskop, north of Vanrhynsdorp.



Fig. 19.25. *T. peculiaris*, PVB 1293, west of Hol River Station.

History

The material that Carl Lückhoff used to describe *T. peculiaris* was collected by P.L. Meiring near Vredendal and it flowered in Cape Town in March 1938. Charles T. Villet also collected it around this time. Villet's material from near Vanrhynsdorp flowered in October 1936 and some that he found near Loeriesfontein flowered

in September and October 1938.

However, this species was discovered much earlier. Examination of the type specimen of *Caralluma intermedia* revealed that some of it was in fact made up of pieces of flowers of *T. peculiaris*. So the Mr. Reynolds who supplied this material to Henry Barkly had actually found this species before 1877 (Bruyns 1983).



Fig. 19.26. *T. peculiaris*, Quaggaskop, north of Vanrhynsdorp.



Fig. 19.27. *T. peculiaris*, PVB 1384, north-west of Loeriesfontein, in habitat, December 1976.

5. *Tridentea virescens*

Tridentea virescens (N.E.Br.) L.C.Leach, Trans. Rhod. Scient. Assoc. 59: 3 (1978).

Stapelia virescens N.E.Br., Hooker's Icon. Pl. 20: t. 1910 B (1890).

Lectotype: South Africa, Karoo, on the road to the diamond fields, Dickson sub Barkly 35 (K).

Stapelia aurea Dinter, Feddes Repert. Spec. Nov. Regni Veg. Beih. 53: 53 (1928).

Type: Namibia, Eendorn, Dinter 5115 (BOL, holo; G, PRE, SAM, iso).

Small succulent to 0.5 m diam. **Stems** 30-150 mm long, 8-15 mm thick, grey-green flecked with purple-brown; **leaf-rudiments** 6-10 mm long, subulate. **Inflorescence** with many flowers developing in rapid succession on erect peduncle 5-45 mm long; **pedicels** 15-80 mm long, 1.5-2.5 mm thick, erect and holding flowers facing upwards; **sepals** 2.5-4.0 mm long, $\pm$ 1.25 mm broad at base, narrowly ovate, acute, sometimes with few slightly clavate marginal cilia. **Corolla** 20-30 mm diam., $\pm$ rotate, deeply lobed; outside pale green to pinkish with 5 slightly darker almost parallel nerves along each lobe; inside bright yellow to greenish yellow, densely papillate-rugose (except in tube), papillae obtusely conical and fused into irregular ridges and longitudinal rows on lobes, each papilla tipped with a minute bristle; **tube** very short and shallowly conical around base of gynostegium, with corolla thickened and becoming papillate around mouth but smooth towards base; **lobes** $\pm$ 8-12 mm long, 7-8 mm broad at base, spreading, ovate, acute, margins strongly reflexed so that convex above, rarely with simple white cilia. **Corona** $\pm$ 6 mm tall, 9 mm broad, bright yellow, raised on short stipe; **outer lobes** 2.5-3.0 mm long, $\pm$ 2 mm broad at base, ascending, deeply trifid; central lobule nearly 2 mm long, $\pm$ deltoid, acute to dentate, channelled towards base on inner face; lateral lobules $\pm$ deltoid, diverging, $\pm$ 1 mm long; **inner lobes** 3-4 mm long, connivent becoming recurved above, terete above anthers, obtuse, near base with ascending laterally flattened $\pm$ deltoid dorsal horn 0.5-2.0 mm long.

Distribution and habitat

Tridentea virescens has an extremely wide distribution from Warmbad in the south-eastern corner of Namibia to Kakamas and Prieska in the Northern Cape and from there southwards via the eastern side of Bushmanland to De Aar and Hopetown. Plants have also been collected several times recently between Beaufort West, Aberdeen and Prince Albert (Bruyns 1990a).

Tridentea virescens seems to be of very sporadic occurrence over this area, though occasionally small populations of up to six plants have been located. Specimens are usually found in stony ground or hard loam in floodplains and they are often associated with shrubs of *Lycium* or the driedoring, *Rhigozum trichotomum*.

TRIDENTEA VIRESCENS

Diagnostic features and relationships

Plants of *T. virescens* may be quite large and some up to 500 mm in diameter have been seen, in which case they consist of many robust, erect stems. The stems are a pale, almost silvery green mottled with purple-brown and this pale colouring can often be used to distinguish them from the ubiquitous *T. gemmiflora*. The relatively long leaf-rudiments, which are similar in length to those of *T. gemmiflora*, are quite widely spaced along the stems.

Florally *T. virescens* is unusual in several respects. The flowers are held facing upwards on erect pedicels and the peduncle that sometimes develops is also erect. Inside, the flowers are bright yellow to greenish yellow without any darker spots or bars and they give off a dreadful smell of old human excrement which rather belies their pretty colour. Unlike the next three species, though, they are relatively small and rarely exceed 25 mm in diameter.

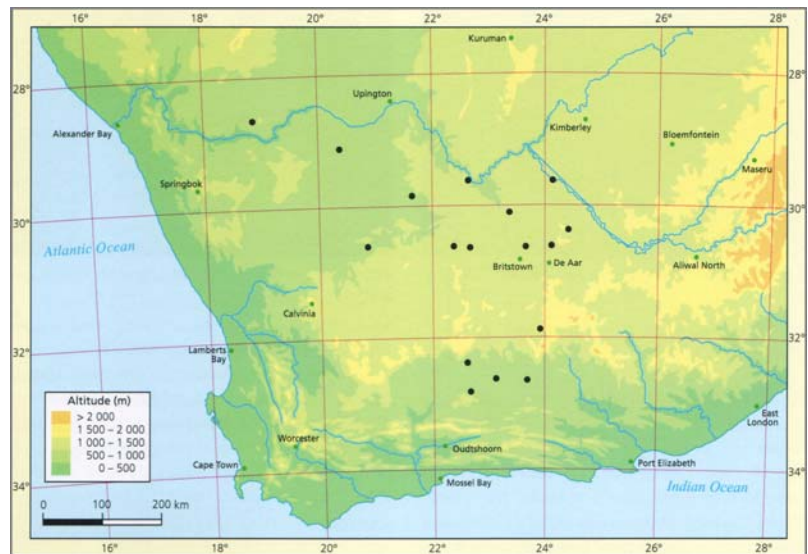


Fig. 19.28. Distribution of *Tridentea virescens*.

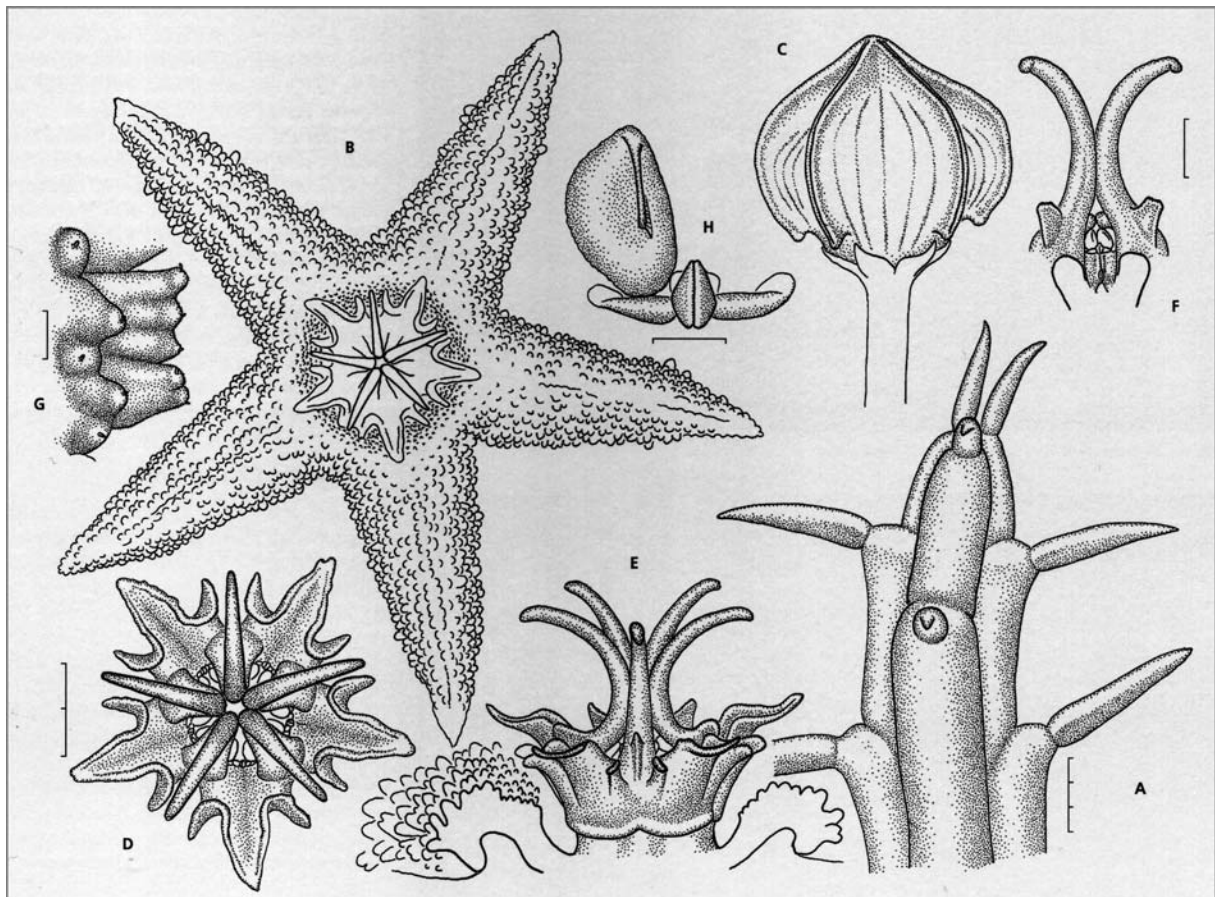


Fig. 19.29. *Tridentea virescens*. A, apex of stem. B, face view of flower. C, bud. D, face view of gynostegium. E, side view of centre of dissected flower. F, inner corona lobes (outer lobe removed). G, papillae inside corolla on lobes. H, pollinarium (one pollinium broken off). Scale bars: A-C, 3 mm (at A); D, E, 2 mm (at D); F, 1 mm; G, 0.5 mm; H, 0.25 mm. Drawn from: PVB 3049, east of Beaufort West.

The corolla is deeply 5-lobed with only a small united portion in the centre which is slightly thickened and forms a shallow and short tube around the base of the gynostegium. Also unusual is the fact that the corolla lobes are convex above from the well-reflexed margins. On the inside the corolla is quite densely covered with prominent papillae which are fused into irregular ridges in which only the apices are free. Each papilla usually has a small and inconspicuous apical bristle.

Nevertheless, despite this very different-looking flower, the gynostegium is indistinguishable from that of, say, *T. pachyrrhiza*, with the customary, broadly trifid outer lobes and long inner lobes with a small, laterally flattened, dorsal fin-like horn. The whole structure is bright yellow and this makes it relatively inconspicuous against the very similar colour of the corolla.

History

Tridentea virescens was first collected by a Mr. Dickson (who also discovered *Duvalia angustiloba*) somewhere in the Great Karoo ('on the road to the diamond fields') between 1873 and 1877. Plants from this collection seem to have been cultivated at Cape Town and flowers from it were drawn by Lady Barkly and pressed for a herbarium specimen. These were later sent to N.E. Brown at Kew and formed the basis of his description. The species was discovered in Namibia by Kurt Dinter on 26 March 1924, but this remains the only collection made in Namibia.



Fig. 19.30. *T. virescens*, PVB 5255, south-west of Kakamas.



Fig. 19.31. *T. virescens*, PVB 3448, north-west of Vanwyksvlei.



Fig. 19.32. *T. virescens*, PVB 5064, 100 km east of Beaufort West.

6. *Tridentea gemmiflora*

Tridentea gemmiflora (Masson) Haw., *Syn. Pl. Succ.* 34 (1812).

Stapelia gemmiflora Masson, *Stap. Nov.* 14, t.15 (1797).

Type: South Africa, Montagu district, in dry places among bushes beyond Platteklief, Masson (missing).

Lectotype: Masson, *Stap. Nov.* t.15.

Stapelia hircosa Jacq., *Stap.* t. 25 (1806-19) [as '*S. hircola*' Poir. in Lam., *Encycl., Suppl.* 5: 234 (1817)].

S. gemmiflora var. *hircosa* (Jacq.) N.E.Br., *Fl. Cap.* 4 (1): 962 (1909).

Lectotype: Jacq., *Stap.* t. 25.

Tridentea stygia Haw., *Syn. Pl. Succ.* 35 (1812).

Stapelia stygia (Haw.) Schult. in Roem. & Schult., *Syst. Veg.* 6: 32 (1820).

Type: *Tridentea stygia* H. (OXF).

Tridentea moschata Haw., *Suppl. Pl. Succ.* 10 (1819).

Stapelia moschata (Haw.) Schult. in Roem. & Schult., *Syst. Veg.* 6: 32 (1820).

Type: unknown.

Stapelia hircosa var. *densa* N.E.Br., *Hooker's Icon. Pl.* 20: sub t. 1910 (1890).

Stapelia gemmiflora var. *densa* (N.E.Br.) N.E.Br., *Fl. Cap.* 4(1): 963 (1909).

Type: Griqualand West, Barkly 10 (sub MacOwan 2263) (SAM).

Small succulent up to 0.5 (-1) m diam. **Stems** 50-150 mm long, 10-15 mm thick; **tubercles** 2-3 mm long; **leaf-rudiments** 5-10 mm long, subulate. **Inflorescence** with flowers developing in rapid to gradual succession on peduncle 5-20 mm long (rarely up to 40 mm); **pedicels** 30-50 (-70) mm long, 2-3 mm thick, ascending to spreading and holding flowers facing $\pm$ horizontally to upwards; **sepals** $\pm$ 5-6 mm long, 2.5-3.0 mm broad at base, acute, sometimes with few short stout colourless marginal cilia. **Corolla** 45-100 mm diam., $\pm$ rotate; outside green, often spotted with purple or brown coalescing towards apices of lobes, with 7 slightly darker almost parallel slightly impressed nerves on each lobe; inside brown to purple-black irregularly mottled with yellowish, rugulose and papillate especially towards centre, papillae dome-shaped to $\pm$ cylindrical obtuse and fused into ridges, each with a darker apical spot (but no bristle); **tube** shallowly conical, with corolla thickened around mouth; **lobes** 20-35 mm long, 20-30 mm broad at base, spreading, ovate-deltate,



Fig. 19.33. *T. gemmiflora*, PVB 5112, east of Lückhoff.

TRIDENTEA GEMMIFLORA

acute, convex above, with crenulate abruptly erect and fleshy margins bearing vibratile cylindrical to subclavate white to dark purple cilia ± 3 mm long. **Corona** ± 7 mm tall, 13–15 mm broad, yellow heavily marked with dark purple to purple-red marked with yellow (on inner lobes), raised on short stipe; **outer lobes** 7–8 mm long, ± 2.5 mm broad at base, ascending, deeply trifid; central lobule 5–6 mm long, linear to narrowly deltoid, truncate to notched, channelled down inner face; lateral lobules slender, subulate, often widely diverging, from half length of central lobule to as long as it; **inner lobes** ± 6 mm long, connivent becoming recurved above, terete above anthers, obtuse, near base with ascending laterally flattened $\pm$ deltoid dorsal horn 1–2 mm long.

Distribution and habitat

Tridentea gemmiflora is of very wide occurrence in South Africa. While it is nowhere particularly common, it is probably most readily encountered in the Worcester-Robertson Karoo and the Little Karoo, where it is known from about midway between Worcester and Robertson eastwards to Oudtshoorn, Willowmore and Steytleville. The southernmost point in its distribution is on the coastal plain south of the Langeberg between Swellendam and Hei-

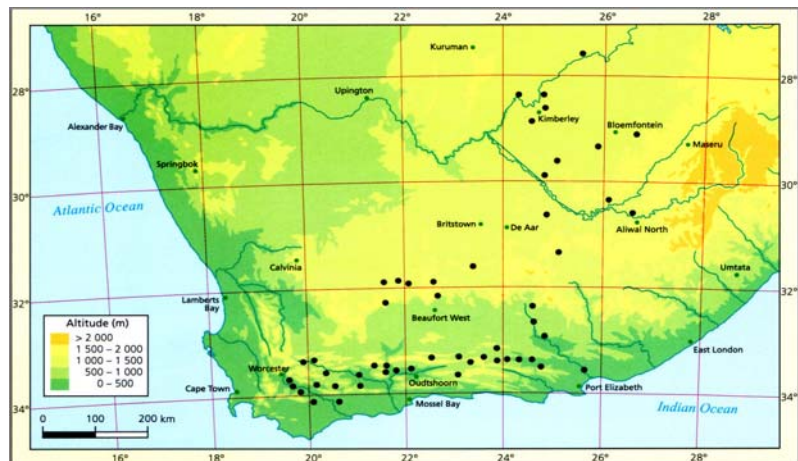


Fig. 19.34. Distribution of *Tridentea gemmiflora*.

delberg. North of the Little Karoo it is of very sporadic occurrence in the Great Karoo from Fraserburg eastwards to Graaff-Reinet and north-east to the Free State around Lückhoff,

with a single record from the southern part of the former Transvaal.

In the Great Karoo plants are usually found under small bushes (often small, spiny *Ruschia*

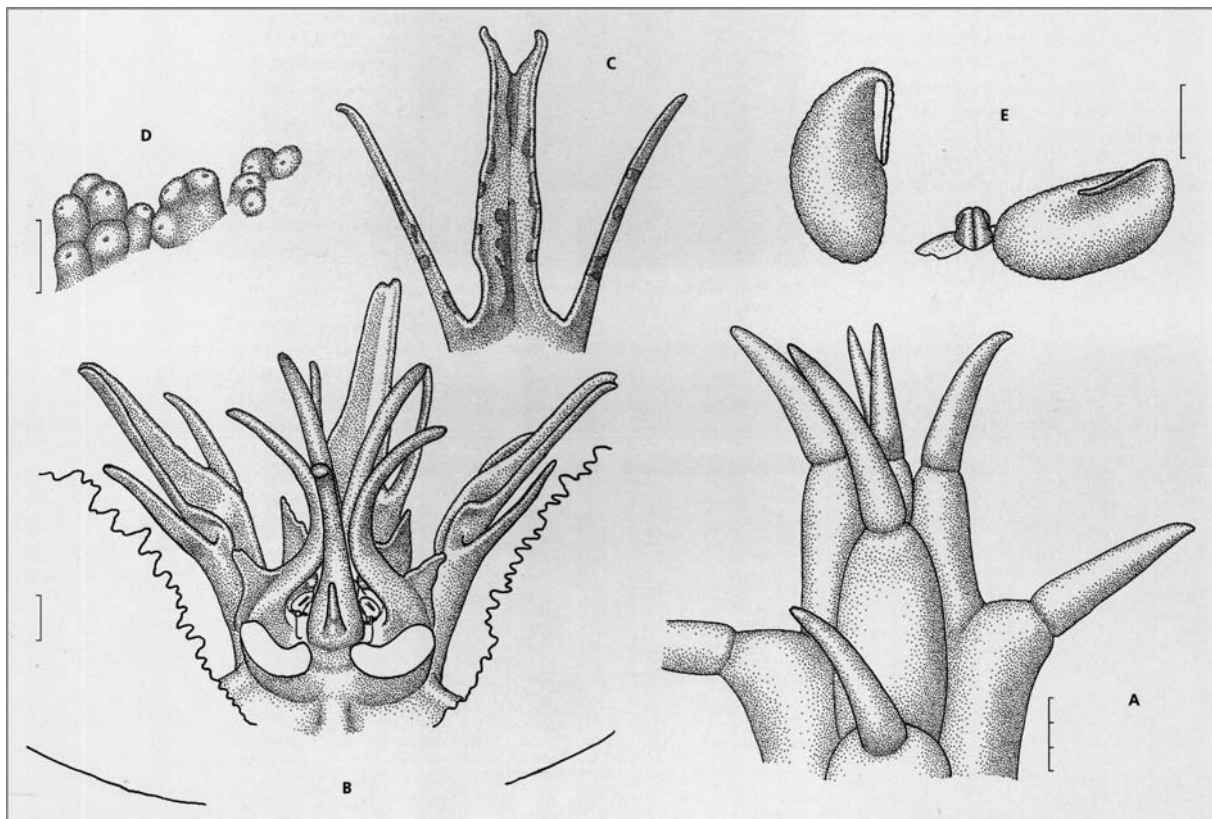


Fig. 19.35. *Tridentea gemmiflora*. A, apex of stem. B, side view of centre of dissected flower, gynostegium with 2 outer corona lobes removed. C, face view of outer corona lobe. D, papillae inside corolla. E, pollinarium (one pollinium broken off). Scale bars: A, 3 mm; B, C, 1 mm (at B); D, 0.5 mm; E, 0.25 mm. Drawn from: A, B, E, PVB 2615, near Avondrust; C, D, PVB 4786, Roodekruis, east of Fraserburg.

plants) on stony, relatively flat ground but further south (in the Little Karoo) it often inhabits slightly sandy spots at the bases of hills among *Acacia* trees or smaller bushes.

Diagnostic features and relationships

Plants of *T. gemmiflora* form a dense cluster of stems which may reach 300 mm in diameter and, depending on the degree to which a specimen is exposed or the stoniness of the terrain, the stems can be extremely densely and tightly packed. Many specimens also bear noticeably thick, older roots.

Amongst those stapeliads with which it grows, the flowers of *T. gemmiflora* are unmistakable. The corolla is not only quite large and usually at least 70 mm in diameter, but it is also remarkably thick and fleshy. The inner surface is usually a rich, deep brown to purple-black and is mostly finely flecked with pale yellow towards the centre. In plants from between Fraserburg and Beaufort West on the western edge of the Great Karoo the mottling with yellow becomes sufficiently dense to dominate the colour of the flower, so that the whole of the inside is then essentially yellow, flecked with purple. In both this species and in *T. pachyrrhiza* the margins of the corolla lobes are quite conspicuously folded upwards. This feature constitutes one of the main differences between these two and *T. marientalensis*.

In *T. gemmiflora* the papillae on the corolla are usually partially fused into clusters. This is similar to the situation in *T. virescens* but the papillae are not as large and consequently the flower does not have such a rough surface. Under the microscope it may be seen that each papilla has only a dark dot or slight knob at the



Fig. 19.36. *T. gemmiflora*, PVB 4902, Soetendalsvlei, east of Klaarstroom.

apex rather than a conspicuous apical bristle as one finds in *T. marientalensis*.

The coronal structure is extremely similar in *T. gemmiflora*, *T. marientalensis* and *T. pachyrrhiza*. The coronas of *T. gemmiflora* and *T. pachyrrhiza* can easily be distinguished by the very short laterals on the outer corona of *T. pachyrrhiza*. The coronas in *T. gemmiflora* and *T. marientalensis* are almost identical. The lobules are all more or less similar in length in the two species but they tend to be somewhat more slender in *T. marientalensis*.

History

Tridentea gemmiflora was discovered by Francis Masson in the western part of the Little Karoo, beyond Platteklouf - in other words in the karroid areas to the north of Gysmanshoek Pass. It is not known when he found it, but it was one of the plants that he took back to England with him in 1795 and he recorded that it flowered at Kew in 1796.



Fig. 19.37. *T. gemmiflora*, PVB 4000, Fraserburg.

7. *Tridentea pachyrrhiza*

Tridentea pachyrrhiza (Dinter) L.C. Leach, *Excelsa* Taxon. Ser. 2:14 (1980).

Stapelia pachyrrhiza Dinter, *Feddes Repert. Spec. Nov. Regni Veg.* 19:154 (1924).

Type: Namibia, Buntveldschuhplato, Dinter 4721 (missing).

Neotype: Namibia, Buchuberge, Dinter 6491 (SAM, holo; BOL, G, GRA, KMG, M, PRE, iso).

Stapelia umbonata Pillans, *S. African Gard. & Country Life* 18: 62 (1928, special reprint).

Type: South Africa, Richtersveld, N.S. Pillans 5809 (BOL, holo; PRE, iso).

Small succulent forming dense clump of tightly packed stems 60-200 mm diam. **Stems** 20-60 (-80) mm long, 10-15 mm thick, greyish green; **tubercles** 2-3 mm long; **leaf-rudiments** 1-2 mm long. **Inflorescence** with flowers developing in rapid to gradual succession on peduncle 5-20 mm long (rarely up to 40 mm); **pedicel** 25-35 mm long, 3-5 mm thick, thickening towards apex, ascending, holding flower facing $\pm$ horizontally to upwards; **sepals** $\pm$ 7 mm long, 3 mm broad at base, ovate, acuminate. **Corolla** 40-75 mm diam.; outside green, often spotted with purple or brown, with spots coalescing towards apices of lobes, with 7 slightly darker almost parallel slightly impressed nerves on each lobe; inside maroon to purple-black irregularly mottled with yellowish, rugulose and papillate especially towards centre, papillae dome-shaped to $\pm$ cylindrical obtuse and fused into ridges, each with a darker apical spot (but no bristle), often white towards apex; **tube** shallowly conical, with corolla thickened around mouth; **lobes** 20-25 mm long, 20-25 mm broad at base, spreading to reflexed, ovate-deltate, slightly convex, with crenulate abruptly erect and fleshy margins bearing subclavate vibratile cilia up to 3.5 mm long. **Corona** $\pm$ 7 mm tall, 13-15 mm broad, yellow heavily marked with dark purple to red-purple marked with yellow (on inner lobes), raised on short stipe; **outer lobes** 4-5 mm long,

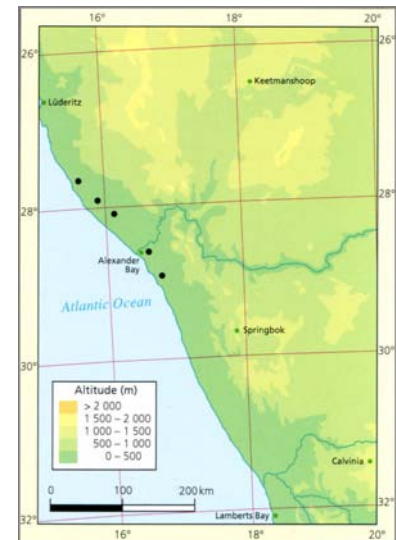


Fig. 19.38. Distribution of *Tridentea pachyrrhiza*.

TRIDENTEA PACHYRRHIZA

2.0-2.2 mm broad at base, ascending, trifid; central lobule $\pm$ 4 mm long, narrowly deltoid, $\pm$ acute, slightly channelled down inner face; lateral lobules deltoid, widely diverging, 0.5-2.5 mm long; **inner lobes** 5-6 mm long, connivent becoming recurved above, terete above anthers, obtuse, near base with ascending laterally flattened dorsal horn 0.7-2.5 mm long and 0.5-1.0 mm broad near base.

Distribution and habitat

Tridentea pachyrrhiza is of very local occurrence and is found around the mouth of the Orange River from north of Port Nolloth in South Africa to near Pomona south of Lüderitz in Namibia. Plants are known only within 20 km of the coast.

The part of the Namib Desert around the mouth of the Orange River has several examples of taxa in the Apocynaceae which occur there in marked isolation from related species. Others are *Cynanchum meyeri*, *Rhyssolobium dumosum* and *Ectadium*, all of which are non-succulent, woody shrubs, unlike the highly succulent *T. pachyrrhiza*.

Plants are usually found in fairly soft, slightly calcareous, yellow to reddish sand and occasionally grow tightly wedged among rocks. They are almost always found completely in the open, where they are fully exposed to the elements and may even be somewhat blasted by windblown sand.

Diagnostic features and relationships

As the name suggests, the very fleshy roots of this species are unusually stout and they may exceed 5 mm in diameter at the base of the plant. However, this is not a unique feature since roots of comparable thickness are also found in both *T. gemmiflora* and *T. marientalensis*. These structures assist in the storage of



Fig. 19.39. *T. pachyrrhiza*, PVB 1317, Muisvlei, south of Alexander Bay, in habitat, June 2004.



Fig. 19.40. *T. pachyrrhiza*, PVB 1317, Muisvlei, south of Alexander Bay, in habitat, June 2004. The upwardly folded margins of the lobes are clearly visible here.

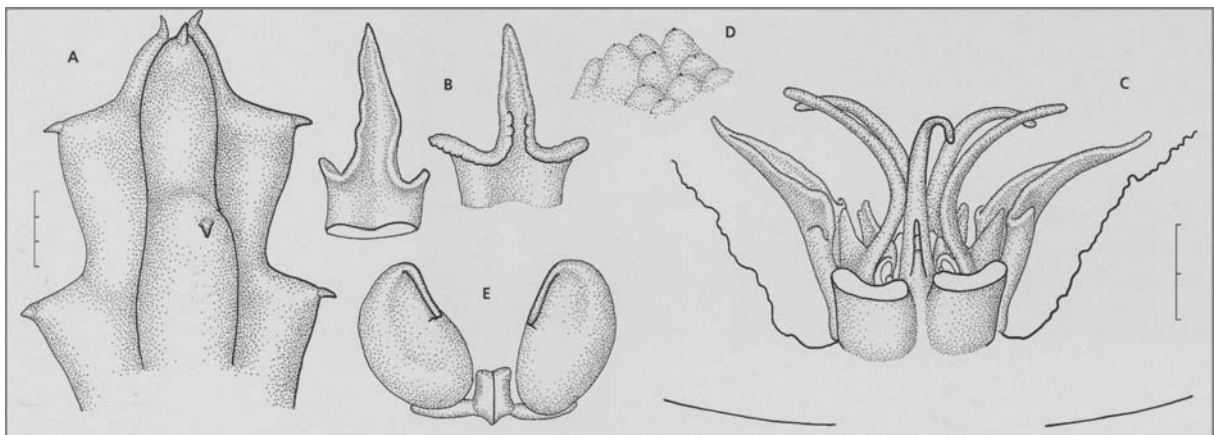


Fig. 19.41. *Tridentea pachyrrhiza*. A, apex of stem. B, face views of two outer corona lobes from different plants. C, side view of gynostegium with two outer corona lobes removed. D, papillae inside corolla tube. E, pollinarium. Scale bars: A, 3 mm; B, C, 2 mm (at C); D, 0.5 mm (at A); E, 0.25 mm (at A). Drawn from PVB 1317, Muisvlei, south of Alexander Bay.



Fig. 19.42. *T. pachyrrhiza*, PVB 1317, Muisvlei, south of Alexander Bay, in habitat, June 2004. Plant with the flower speckled all over with pale yellow.



Fig. 19.43. *T. pachyrrhiza*, PVB 1317, Muisvlei, south of Alexander Bay, in habitat, June 2004.

moisture but might also tend, as they contract in dry conditions, to pull the plant downwards into the fairly loose surrounding ground.

In *T. pachyrrhiza* the stems are short and form dense, compact clumps. Very occasional specimens growing under bushes have longer and less tightly clustered stems. Although the plants are not actually rhizomatous, most of the stem is usually beneath the surface of the sand. This hints at the even more highly adapted habit of *Fenestraria* (Aizoaceae) with which *T. pachyrrhiza* may occur on occasion, where the stems are wholly buried beneath the sand and only the tips of the leaves reach the surface. As in the case of *Fenestraria*, plants of *T. pachyrrhiza* may become completely covered by wind-blown sand, especially when they shrivel and pull themselves downwards during dry periods. With the onset of rains the stems swell out and their tips again become visible. This is the state in which this species is usually seen, i.e. with only the tips of the stems visible, so plants are mostly relatively inconspicuous.

Flowering in *T. pachyrrhiza* usually takes place in June or July after the first rains have fallen. There are often several flowers on each inflorescence open at once. They are comparatively large relative to the parts of the plant above the ground and, if several are present, they can hide the plant almost completely. The inside of the very fleshy and somewhat convex

corolla is deep maroon to nearly black, with only a fine reticulation of yellow towards the centre. Flowering specimens are therefore considerably more conspicuous than the plants are normally and the clusters of flowers can be visible for some distance. They emit a weak, excrement-like odour.

Tridentea pachyrrhiza is very similar indeed to *T. gemmiflora*. The most obvious differences lie in the pale grey, much shorter stems with very much shorter leaf-rudiments in *T. pachyrrhiza*. Differences in the flowers are more difficult to see and are mainly found in the outer corona lobes which have a short, narrow central lobule and very short lateral lobules which mostly hardly extend beyond the thickened base of the lobe.

History

Tridentea pachyrrhiza was first observed by M. Kurt Dinter during his expedition of 19 July to 12 October 1922 to the Namib Desert south of Lüderitz. He seems to have seen it in several places near the coast, including the Buntfeldtschuh Plateau and the Buchuberg, where he saw it in 1929 on a second expedition to this area. In South Africa it was first collected by N.S. Pillans in October 1926 in the Richtersveld and he named this material *Stapelia umbonata*.



Fig. 19.44. *T. pachyrrhiza*, PVB 1317, Muisvlei, south of Alexander Bay, in habitat, June 2004.

8. *Tridentea marientalensis*

Tridentea marientalensis (Nel) L.C. Leach, Trans.

Rhod. Scient. Assoc. 59: 3 (1978).

Stapelia marientalensis Nel, *Kakteenkunde* 1935:118 (1935).

Type: Namibia, Haruchas, *Berger sub STE 7044*

(missing).

Neotype: Namibia, Haruchas, *Leistner 1819* (PRE, holo; KMG, iso).

Small succulent forming a loose clump up to 0.5 m diam. **Stems** 50-150 mm long, 10-15 mm thick; **leaf-rudiments** 5-12 mm long. **Inflorescence** with few flowers from spreading peduncle 5-100 mm long and 4-7 mm thick; **pedicel** (50-) 70-100 (-130) mm long, often spreading with upturned apex so that flowers humifuse; **sepals** 6-7 mm long, 2 mm broad at base, ovate-lanceolate, acuminate. **Corolla** ± 50-75 mm diam., rotate to slightly campanulate; outside pale green sometimes suffused with purple; inside cream to pale yellow often speckled with brownish maroon towards centre darkening towards middle of lobes and becoming brownish to pinkish maroon towards tips, covered densely below bases of lobes and as far as mouth of tubelet around gynostegium with obtuse conical papillae each tipped with a slightly clavate usually white bristle up to 2 mm long (papillae reaching max. length just beyond mouth of tube, becoming shorter towards bases of lobes); **tube** shallowly conical, with corolla somewhat thickened except just around gynostegium; **lobes** 18-25 mm long, 12.5 mm broad at base, spreading to strongly reflexed, ovate, acute, margins with white to purple subclavate vibratile cilia up to 5 mm long. **Corona** ± 7 mm tall, 10-12 mm broad, pale yellow spotted with brown, raised on short stipe; **outer lobes** ± 6 mm long, 1.5-2.0 mm broad at base, ascending, deeply trifid; central lobule ± 5 mm long, narrowly deltoid, acute to truncate or bifid, slightly channelled down inner face; lateral lobules slender, subulate, often widely diverging, 3.0-3.5 mm long; **inner lobes** 3.5-5.0 mm long, connivent becoming recurved above, terete above anthers, obtuse, near base with ascending laterally flattened ± narrowly deltoid dorsal horn 1.0-2.5 mm long and 0.5-0.6 mm broad near base.

Although it is not a well-known species, *T. marientalensis* is in fact quite widespread. The localities indicated on the map are scattered and relatively few but this is probably mainly because little collecting has been done in the region concerned, which is fairly remote. It is known to occur from west of Helmeringhausen and Maltahöhe in southern Namibia across to Warmbad and Mariental, from there eastwards into Botswana around Tsabong and south-eastwards in South Africa to near Olifantshoek. Over much of this area it is quite rare but periodically patches may be encountered where it is locally very common.

In Namibia it is usually found on reddish Kalahari sand, on calcrete or even among granitic gravel. In areas with dunes it grows in the firmer, low-lying, more stable areas between them. Over most of this region it is particularly associated with stands of the ubiquitous *drie-*

TRIDENTEA MARIENTALENSIS

doring, *Rhigozum trichotomum*, which covers vast areas of southern Namibia and the arid parts of the Northern Cape, outside the winter-rainfall area.

In South Africa and Botswana *T. marientalensis* appears also to be found mainly in flattish areas and here it is generally also associated with *R. trichotomum* and *Acacia* scrub, usually on reddish sands or calcrete.

Plants of *T. marientalensis* may often be quite large and clumps up to 0.5 m in diameter have been seen several times in Namibia. Except for a slightly paler colour, the stems cannot be distinguished from those of *T. gemmiflora* and they have, as well, very similar, quite long leaf-rudiments on the younger stems. The pedicels are relatively long (longer than in *T. gemmiflora*) and usually lie on the surface of the ground around the plant with the flower facing partly upwards at their ends. They develop from a spreading peduncle, about half as thick as the stems, which persists over several years and

may ultimately reach 100 mm long. *Tridentea marientalensis* is particularly floriferous and when a large plant comes into flower it can sometimes be surrounded by a ring of flowers on the ground.

Although the flowers of *T. marientalensis* usually have a distinctive paler area towards the centre, their colour may sometimes approach that of *T. gemmiflora*. The two species differ, among other things, in the very much longer pedicels and generally smaller flowers of *T. marientalensis*. In *T. marientalensis* the corolla lobes are also narrower relative to their length, they are usually more noticeably convex and do not have a flap of tissue folded upwards along the margins. In both species the inside of the corolla is papillate but in *T. marientalensis* the papillae are discrete and not fused into groups as in *T. gemmiflora*. In *T. marientalensis* each papilla has a fairly long apical bristle, which is absent in *T. gemmiflora*.

8a. *Tridentea marientalensis* subsp. *marientalensis*

Stapelia auobensis Nel in A.C. White & B. Sloane, *Stap.*, ed. 2, 2: 472 (1937).

Type: Namibia, Auob River, *Triebner sub STE 2106* (missing).

Lectotype (selected here): White & Sloane, *Stap.*, ed. 2, 2: fig. 411.

Corolla almost flat; inside sparsely yellowish towards centre, becoming reddish to blackish beyond; **tube** short, more or less funnel-shaped.

Distribution and habitat

In eastern Namibia subsp. *marientalensis* is found in the area between Leonardville, Stampriet and Aroab. It is known as well in the adjacent part of Botswana but has only been collected around Tsabong and is almost certainly more widely distributed there than the records indicate at present. In the Northern Cape of South Africa it has been gathered around the Kalahari Gemsbok National Park, south to Augrabies Falls and eastwards to near Olifantshoek.

Key to the subspecies of *T. marientalensis*

- | | |
|---|----------------------------------|
| Corolla ± flat, inside sparsely yellowish towards centre | 8a. subsp. <i>marientalensis</i> |
| Corolla shallowly campanulate, inside yellow to cream except beyond upper half of lobes | 8b. subsp. <i>albipilosa</i> |



Fig. 19.45. *T. marientalensis* subsp. *marientalensis*, PVB 5451, Auob River north-east of Koës, Namibia.

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History

The first recorded collection of subsp. *albipilosa* seems to be one that was made by Joseph Archer in February 1929 at Klein Karas. It was

also gathered several times by Waldemar Felix Bayer (who was at that time the magistrate in Warmbad) in April 1939 in the Bondelswart Reserve, to the south-west of Karasburg. Material was first recorded much further to

the west, near Maltahöhe, by Giess, Volk and Bleissner (Mrs. Giess) in 1963 and a specimen collected by W. Giess at the eastern foot of the Tiras Mountains was later described by him as *Stapelia albipilosa*.



Fig. 19.50. *T. marientalensis* subsp. *albipilosa*, PVB 5685, south-west of Maltahöhe, Namibia, in habitat, at the base of a driedoring (*Rhigozum trichotomum*), March 1993.

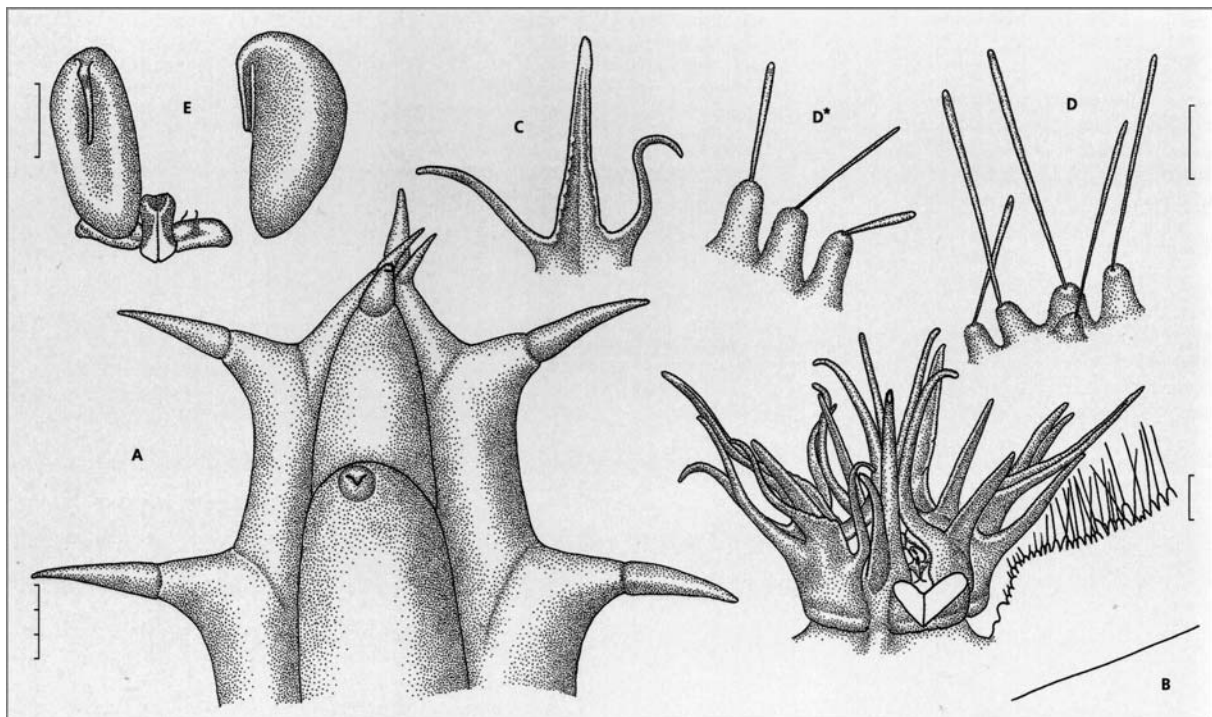
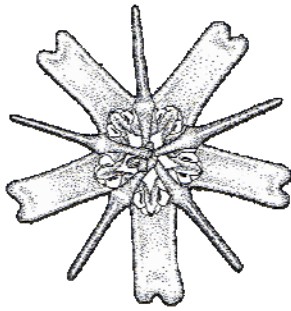


Fig. 19.51. *Tridentea marientalensis* subsp. *albipilosa*. A, apex of stem. B, side view of centre of dissected flower, gynostegium with one outer corona lobe removed. C, face view of outer corona lobe. D, papillae inside corolla. E, pollinarium (one pollinium broken off). Scale bars: A, 3 mm; B, C, 1 mm (at B); D, 0.5 mm; E, 0.25 mm. Drawn from: A-E, PVB 4220, Tiras, Namibia; D*, PVB 4169, Rooiberg Suid, south-west of Maltahöhe, Namibia.

20. Tromotriche



In 1812 Haworth moved *Stapelia pruinosa*, *S. glauca* and *S. revoluta* to a new genus *Tromotriche*. The genus was named for the fringe of trembling, spatulate cilia along the margins of the lobes which are present in *Stapelia revoluta* and its synonym *S. glauca* but are

actually not known in *S. pruinosa* (now known as *Quaqua pruinosa*). Sweet transferred a few more species to *Tromotriche* but the name did not enter common usage and it was relegated to an informal section of *Stapelia* by J.A. Schultes and by Stephan L. Endlicher (1836-40). It was formally established as a section of *Stapelia* by Decaisne (Decaisne 1844). In 1982 Leach resurrected *Tromotriche* and placed in it the three species *Stapelia engleriana*, *S. revoluta* and *S. thudichumii*. A detailed investigation of *Tridentea* and *Tromotriche* (Bruyns 1995a) showed that *S. engleriana* fitted far better into *Stapelia* and that some of the species included by Leach in *Tridentea* were more closely related to *S. revoluta* and *S. thudichumii* than to others in *Tridentea*. Therefore *Tromotriche* was again modified to include these nine species, while *S. engleriana* was referred back to *Stapelia*. The species *T. baylissii*, *T. choanantha* and *T. longii* were considered to be most closely related to *T. revoluta* and *T. thudichumii* and were placed in sect. *Tromotriche*, while the remaining six

species were placed in sect. *Caruncularia*. This name was originally given to a separate genus in which Haworth included just *Stapelia pedunculata*.

On the basis of morphological features, it was suggested in Bruyns (1995a) that *Stapelia* and *Tromotriche* may be closely related. The molecular investigation by Meve & Liede (2002), involving only *T. longipes* and *T. ruschiana*, revealed nothing about the relationships of *Tromotriche* or about relationships within it. Our own molecular research, in which all species were included, has revealed unexpected complexity here. The 'Richtersveld group', consisting of *T. aperta*, *T. herrei*, *T. pedunculata*, *T. ruschiana* and *T. umdausensis*, forms a well-supported branch, as does a smaller branch consisting of *T. baylissii* and *T. choanantha*. *Tromotriche longii* is nested within *Orbea*. *Tromotriche revoluta* and *T. thudichumii* form two further separate branches. The relationships between these groupings and between them and other genera

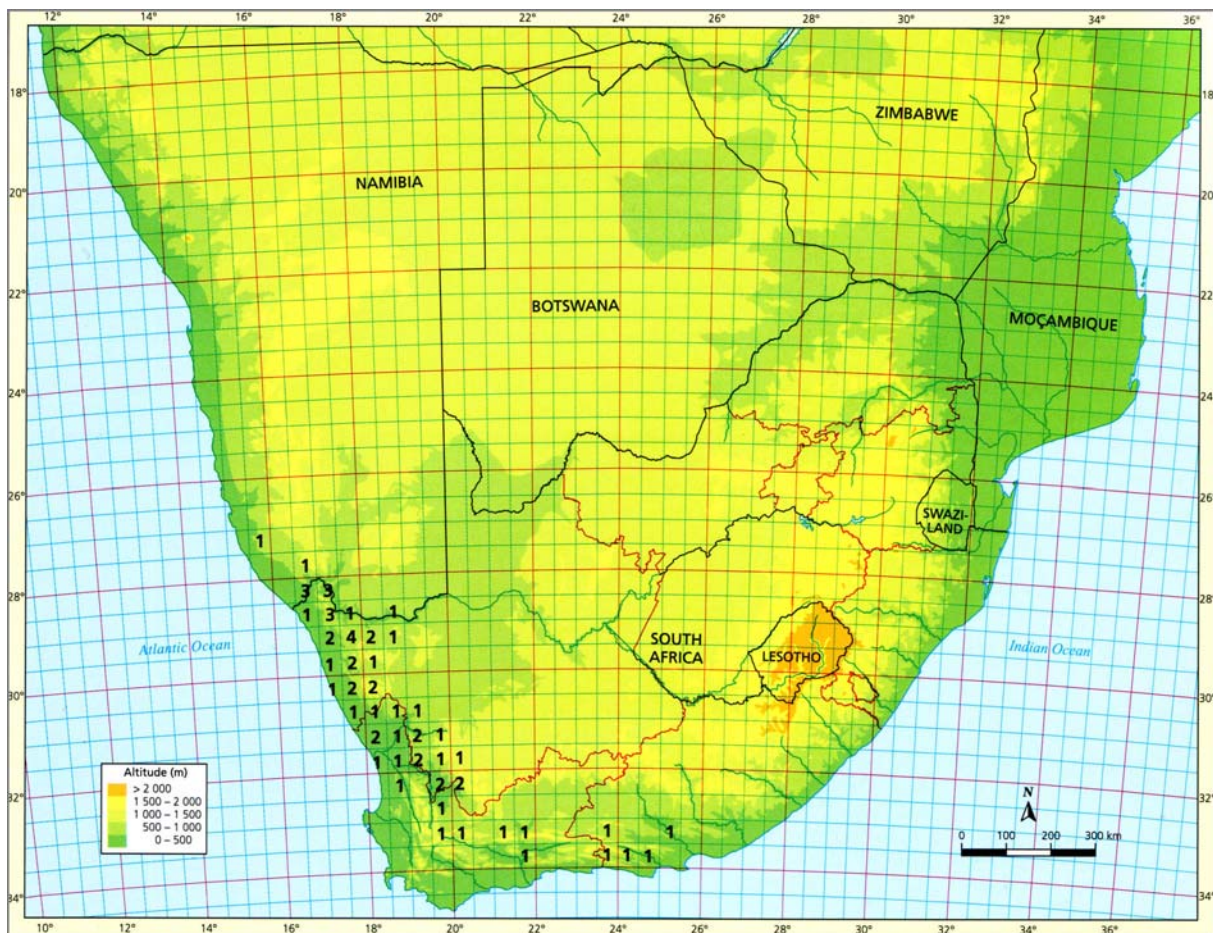


Fig. 20.1. Patterns of diversity in *Tromotriche*, showing the number of species recorded to date in each half-degree square.

TROMOTRICHE

remain unresolved, and it appears that this is a case where further gene-regions are required to resolve the situation. For the present, all these species except *T. longii* are retained in *Tromotriche*, though future work may show that they are not closely related, especially since the definition of the genus rests partly on the absence of certain structures rather than on their presence. *T. longii* has been moved to *Orbea*.

Here 9 species of *Tromotriche* are recognised, reduced from the 11 which were dealt with in Bruyns (1995a). The genus is recognised particularly by the very rounded angles and the rounded, obtuse tubercles on the stems, as well as by the minutely papillate surface of the stems. The almost total absence of any leaf-rudiments is also characteristic.

Tromotriche Haw., *Syn. Pl. Succ.*: 36 (1812).

Stapelia [unranked] *Tromotrichae* Schult. in Roem. & Schult., *Syst. Veg.* 6: 34 (1820).

Stapelia sect. *Tromotriche* (Haw.) Decne. in DC, *Prodr.* 8: 657 (1844).

Lectotype: *Tromotriche revoluta* (Masson) Haw.

Caruncularia Haw., *Syn. Pl. Succ.*: 333 (1812).

Stapelia [unranked] *Carunculariae* Schult. in Roem. & Schult., *Syst. Veg.* 6: 46 (1820).

Stapelia sect. *Caruncularia* (Haw.) Decaisne in DC, *Prodr.* 8: 658 (1844).

Tridentea sect. *Caruncularia* (Haw.) L.C. Leach, *Exceisa Taxon. Ser.* 2: 5 (1980).

Tridentea sect. *Caruncularia* subsect. *Claviculares* L.C. Leach, *Excelsa Taxon. Ser.* 2: 5 (1980).

Tromotriche sect. *Caruncularia* (Haw.) Bruyns, S. *African J. Bot.* 65: 306 (1999).

Type: *Caruncularia pedunculata* (Masson) Haw. [= *Tromotriche pedunculata* (Masson) Bruyns].

Tridentea sect. *Caruncularia* subsect. *Apertae* L.C. Leach, *Excefea Taxon. Ser.* 2: 5 (1980).

Type: *Tridentea aperta* (Masson) L.C. Leach [= *Tromotriche aperta* (Masson) Bruyns].

Tridentea sect. *Caruncularia* subsect. *Pendentes* L.C. Leach, *Excefea Taxon. Ser.* 2: 5 (1980).

Type: *Tridentea baylissii* (L.C. Leach) L.C. Leach [= *Tromotriche baylissii* (L.C. Leach) Bruyns].

Small spineless succulent, sometimes forming compact clump, sometimes extensively rhizomatous with widely separated above-ground stems, occasionally with stems creeping or pendulous (from ledges on cliffs). **Stems** decumbent to prostrate, fleshy and firm, glabrous with matt surface, 40 mm-3 m long, 4-20 mm thick, green to grey-green or purple-green sometimes flecked with brown; **tubercles** 1-3 mm long, obscure and obtuse, laterally slightly flattened and joined into 4 (-6) very broadly rounded obtuse angles along stem which is then subtessellate or even almost cylindrical, rarely each tipped with small deltoid tooth (< 1 mm long) subtended by 2 stipular denticles and mostly without teeth or stipules. **Inflorescences** glabrous, 1 to several per stem, arising between apex and base of stem, bearing 1-5 flowers developing in gradual succession on stout gradually

lengthening peduncle 1-50 mm long with several lanceolate bracts 1-2 mm long (sometimes with small lateral teeth); **pedicel** (6-) 10-190 mm long, 1.5-4.0 mm thick, spreading to ascending; **sepals** 2-8 mm long, 1-2 mm broad at base, lanceolate, acute. **Corolla** (12-) 15-70 mm diam., rotate to campanulate or tubular-campanulate, deeply to shallowly lobed; outside glabrous and smooth; inside glabrous, often reticulately to transversely rugose, usually with small unicellular papillae especially in tube; **tube** shallowly to deeply conical, with corolla much thickened around mouth and sometimes raised into very thick annulus; **lobes** 5-30 mm long, 5-16 mm broad at base, ascending to spreading, acute, convex above with margins folded downwards, margins usually with vibratile cilia. **Corona** 3-10 mm tall, 4-11 mm broad, consisting of 2 series arising on staminal tube and mostly slightly intergrown only near bases, glabrous, raised on short stout pentagonal stipe; **outer lobes** 1.0-3.5 mm long, ascending to spreading, simple, dorsiventrally flattened and usually channelled down middle, fused to inner lobes at base only or fused laterally to lower sides of inner lobes to form cup beneath guide-rails; **inner lobes** 0.7-6.0 mm long, adpressed to backs of anthers at least in lower half of anthers, usually much exceeding them and rising above centre of style-head, dorsiventrally flattened at least towards base (often cylindrical or clavate and variously tuberculate above), mostly with laterally flattened deltoid to clavate dorsal horn in lower half. **Anthers** horizontal on top of style-head, margins shrinking back to expose pollinia, rectangular. **Pollinium** D-shaped, longer than broad, insertion-crest twisting from outer edge onto dorsal surface, caudicle attached with broad cupular pad to base. **Follicles** erect, terete-fusiform, obclavate, slender to stout, with horns diverging at 30-180°, longitudinally mottled with narrow broken purple stripes, glabrous, smooth.

In *Tromotriche* there is much variation in habit. In *T. herrei* and *T. umdausensis* the plant is compact and the stems are erect with only a short horizontal portion at the base. *Tromotriche aperta*, *T. pedunculata* and *T. ruschiana* have a somewhat spreading to ascending habit with occasional horizontal stems, so plants can be slightly more diffuse.

In *T. revoluta* and *T. thudichumii* the stems are strongly rhizomatous, with underground runners spreading away from the often small main plant for some distance before rising and appearing above the surface. One might suspect that this rhizomatous habit is a response to sandy habitats. If this were the case for *T. revoluta*, one would expect it to be common in the arid coastal *sandveld* between Elands Bay and Port Nolloth or in the deep red sands along the lower Olifants River. However, my own investigations have not turned it up in these areas at all: north of the Olifants River it is most common on the Knersvlakte on small stony outcrops and on the steep, rocky slopes of the escarpment on the eastern boundary of the Knersvlakte. Only around Clanwilliam is it quite common in the white to yellow sand along the Olifants River, but it does not appear to grow further west of this in the *sandveld*. Along the

Olifants River it sometimes forms dense clumps of stems, quite unlike the widely scattered single stems found in rocky habitats.

Similarly, *T. thudichumii* is not known in sandy habitats. Neither rockiness nor hardness of the soil seem to have the slightest inhibiting effect on the plants being rhizomatous. Consequently, there are no grounds for believing that, amongst the stapeliads, this growth form is a response to sandy habitats, just as it is not a response to fire either (see *Duvalia*).

A more exotic habit is found in *T. baylissii*, *T. choanantha*, where the plants are often (in *T. baylissii* nearly always) pendulous from ledges on cliffs and where individual stems may reach 3 m long. A rhizomatous habit is to some extent present also in these species. The plants all have the ability to grow horizontally and creep beneath leaf-litter and small stones on ledges and flattish spots in the steep areas where they normally occur. It is probable that the very long stems that sometimes arise in *T. baylissii*, for example, are a phenomenon similar to the long horizontal runners in *T. revoluta*.

In *Tromotriche* the stems are grey-green to purplish, sometimes mottled with brown. They have fairly low, rounded tubercles which are joined into (mainly) four obtuse and rounded angles along the stem, often giving the stems a somewhat tessellate appearance. The angles along the stems are only really conspicuous in *T. revoluta*.

Each tubercle bears a small deltoid ridge at its apex (just below the next tubercle) and, in *T. revoluta* and *T. thudichumii* only, this ridge is flanked by two small stipular denticles which appear to be somewhat glandular. A leaf-rudiment with any kind of recognisable structure is completely absent.

In all species the surface of the stem is somewhat rough. This is caused by the fact that the outer walls of the epidermal cells are raised into papillae and, as in *Stapelia* and some *Piранthus*, these papillae too are often raised on low mounds by the surrounding cells. While these papillae are never as long as in a typical *Stapelia*, they may be comparable to papillae found in some stapelias with almost glabrous stems. The roughness of the surface is most pronounced in *T. thudichumii*, where the stems have a distinctly sandpapery texture, and is least obvious in *T. revoluta*, where the stems are relatively smooth and also often markedly greyish with a waxy covering.

The position of the inflorescence is particularly variable in *Tromotriche*. In *T. aperta*, *T. pedunculata* and *T. ruschiana* inflorescences are found mainly near the bases of the stems and then they are mostly solitary, bearing few, relatively large flowers. In the other species they may arise anywhere between the base and the apex of the stem (and then there is often more than one per stem and each consists of

several flowers developing in succession). In *T. thudichumii*, for example, there may be up to six inflorescences on a stem and they are often around its apex.

Flowers in *Tromotriche* vary mainly between 15 and 50 mm in diameter and are especially variable in the shape of the corolla. This is flat to slightly reflexed in *T. pedunculata* and *T. thudichumii*, campanulate but with a short tube in *T. aperta*, *T. revoluta*, *T. ruschiana* and *T. umdausensis*, campanulate with a deeper tube in *T. herrei* and even more deeply tubular-campanulate in *T. baylissii* and *T. choanantha*. There is always a thickened annulus in the corolla, which is located in all cases some distance below the fusion of the lobes. This annulus is not nearly as conspicuous here as it is in some species of *Orbea* and the corolla generally has to be dissected before it can be seen properly. When the corolla is dissected, it will be seen that the annulus is relatively thin in *T. herrei*, *T. thudichumii* and *T. umdausensis* but is thicker in *T. aperta*, *T. baylissii* and *T. choanantha* and really quite massive in *T. pedunculata* and *T. revoluta*. In some cases (notably in *T. aperta*, *T. baylissii*, *T. choanantha*, *T. pedunculata* and *T. revoluta*) it spreads inwards and slightly downwards over the base of the tube, which is then more or less flat around the stipe on which the gynostegium stands.

Below the annulus there is a shallow, bowl-shaped to cupular tube around the gynostegium. This is particularly short in *T. baylissii* and *T. choanantha*, where the annulus sits it almost to the base. The corolla tube could therefore again be said to consist of two parts: a fused 'secondary' tube below the bases of the lobes and above the thickened annular portion and the 'primary' tube below the annulus. In *T. thudichumii* the fused portion below the lobes is more or less flat but in *T. baylissii*, *T. choanantha* and *T. herrei* it forms the upper part of the corolla tube.

In most species, except *T. choanantha* and *T. herrei*, small, clavate, unicellular papillae are found with varying density over the inside of the flower, often mainly in the tube (fig. 27 A). In many species the inside of the corolla is also raised into transverse and parallel or reticulated ridges and this reaches its most spectacular form in *T. herrei*. Vibratile, clavate cilia are often present along the margins of the lobes.

The gynostegium is always raised above the base of the tube on a pentagonal stipe which is particularly long in *T. revoluta* and *T. thudichumii*. The corona consists of two series of lobes. In most species the outer lobes are narrow and channelled above (very small relative to the inner lobes in *T. herrei*, *T. pedunculata* and *T. ruschiana*) and do not spread at all around the gynostegium behind the inner lobes. However, in *T. aperta* and *T. umdausensis*, where the outer lobes are particularly short and, in fact, merely fill the gaps between the inner lobes, they form a more or less continuous cup around the gynostegium. As is usual, the inner lobes are dorsiventrally flattened above the anthers and they vary from short and not rising at all in *T. umdausensis* to comparatively long in most of the others. They generally become cylindrical above, and are sometimes clavate with a swollen apex. A dorsal horn is usually present and is always laterally flattened towards the base. In several species its apex is swollen too, so its shape is then very similar to that of the lobe itself.

The pollinaria are medium-sized, with somewhat D-shaped pollinia. These are singularly long and narrow in *T. baylissii* and *T. choanantha*, probably in response to the narrowness of the tube and the small spaces available between the corona lobes, as is also found in *Stapelia flavopurpurea*. On the pollinium the insertion-crest is twisted onto the dorsal surface, and in all species the corpuscle is prominently broadened towards its apex.

Tromotriche occurs almost exclusively

within the winter-rainfall zone of the western part of South Africa and south-western Namibia. It also appears to be fairly strictly contained by the western and southern edge of the 'Karoo dolerite plate' (except for *T. thudichumii*, which occurs on doleritic slopes in the north-eastern Ceres Karoo and beyond). The genus with most similar distribution to this is *Quaqua*. The extremities of the two distributions correspond closely, though *Quaqua* is more common in the Little Karoo and in the south-western Cape and shows some tolerance for dolerites on the Roggeveld Plateau.

In *Tromotriche*, only *T. pedunculata* could be considered to be widely distributed. The species are mostly concentrated in Namaqualand towards the eastern edge of the Richtersveld (where up to four per half-degree square are found) and this is mainly brought about by the occurrence there of *T. pedunculata* and three species (*T. aperta*, *T. herrei* and *T. umdausensis*) which are rather more restricted. These species are peculiar for their frequent occurrence in fields of quartz gravel. This is especially the case for *T. herrei* and *T. umdausensis*, the only *stapeliads* that are regularly found in this type of habitat. Closely related to these species in the Richtersveld is another very local one, *T. ruschiana*, which occurs to the north of all of them and somewhat isolated from the others.

Further south, the Knersvlakte with part of the Olifants River Valley and the Ceres Karoo each have their own unique and 'more or less endemic' species of *Tromotriche*. The remainder of the distribution of the genus lies considerably further south and is made up of two remarkable disjunct patches deep within the sandstone mountains of the Cape Fold System. Each of these species is very local in its occurrence, though recent exploration has proved them to be more widely distributed than was formerly known (Leach 1980a).

Key to the species

1. Inner corona lobes with laterally flattened dorsal horns 2.
2. Corolla tubular-campanulate 3.
3. Corolla smooth inside, inner corona lobes not thickened towards apex 9. *T. choanantha*
3. Corolla transversely rugulose inside, inner corona lobes slightly thickened towards apex 8. *T. baylissii*
2. Corolla $\pm$ turban-shaped or rotate-reflexed 4.
4. Corolla 20–30 mm diam., inner corona lobes shorter than outer with dorsal horn equalling or exceeding length of lobe 2. *T. thudichumii*
4. Corolla (30–) 40–50 (–70) mm diam., inner corona lobes much larger than outer, with dorsal horn much shorter than lobe 1. *T. revoluta*
1. Inner corona lobes with clavate dorsal horn or horn absent 5.
5. Inner corona lobes and their dorsal horns both nearly equal in length and both prominently clavate 6.
6. Corolla rotate and with tube $\pm$ 2 mm long 3. *T. pedunculata*
6. Corolla rotate-campanulate, tube 8–15 mm long 7.
7. Corolla lobes with marginal cilia, tube with small unicellular papillae inside 4. *T. ruschiana*
7. Corolla lobes eciliate, tube without papillae inside 7. *T. herrei*
5. Inner corona lobes at most slightly thickened above and without dorsal horn 8.
8. Inner corona lobes seldom exceeding anthers, without clavate tips 5. *T. umdausensis*
8. Inner corona lobes much exceeding anthers, produced above them and slightly thickened towards tips 6. *T. aperta*

TROMOTRICHE REVOLUTA

1. *Tromotriche revoluta*

Tromotriche revoluta (Masson) Haw., *Syn. Pl. Succ.*: 36 (1812).

Stapelia revoluta Masson, *Stap. Nov.*: 12, t.10 (1796).

Type: South Africa, Cape, Namaqualand, Knersvlakte, Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t.10.

Stapelia glauca Jacq., *Stap.*: t. 44 (1806-19).

Lectotype: Jacq., *Stap.*: t. 44.

Tromotriche glauca Donn ex Haw., *Syn. PL Succ.*: 37(1812).

Neotype (selected here): '*Stapelia reclinata glauca*' (OXF).

Stapelia tigridia Decne. in DC, *Prodr.* 8: 657 (1844).

Stapelia revoluta var. *tigridia* (Decne.) N.E.Br.,

Fl. Cap. 4(1):981(1909).

Lectotype: Bot. Mag. 19: t. 724 (1804).

Stapelia revoluta var. *glaucescens* Rust ex A.Berger, *Stap. u. Klein.*: 228 (1910).

Type: unknown.

Few-stemmed to clump-forming succulent up to 1 m diam, sometimes forming large patches (to 2-3 sq m in extent) of scattered single stems. **Stems** 40-200 (-500) mm long, 15-30 mm thick (usually cylindrical and at most 10 mm thick below ground), decumbent, often spreading horizontally underground for up to 1 m, above-ground parts pale bluish green to grey-green; **tubercles** 2-3 mm long, joined into 4 broad obtuse angles along stem, each tipped with small deltoid tooth (< 1 mm long) flanked by 2 minute denticles, tooth and denticles with time becoming covered with grey cork-like callus. **Inflorescence** 1 (-3) per stem arising towards apex, bearing 1-2 flowers developing in gradual succession $\pm$ without peduncle, with few short deltoid acute bracts 1.5-2.5 mm long; **pedicel** 5-15 mm long, 2-3 mm thick, spreading and holding flower facing horizontally; **sepals** 6-8 mm long, 1.5-2.0 mm broad at base, lanceolate, acute. **Corolla** (30-) 40-50 (-70) mm diam., $\pm$ turban-shaped; outside pale green suffused with red; inside yellow to red-brown becoming paler to cream on annulus and in tube, smooth and somewhat shiny, with fine acute papillae in base of tube; **tube** $\pm$ 5 mm long, 6-10 mm broad, pentagonal to circular at mouth, cupular and much constricted at mouth by massive overhanging ledge of annulus, formed entirely by much thickened

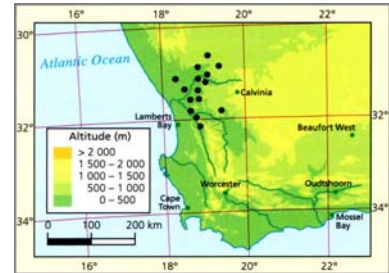


Fig. 20.2. Distribution of *Tromotriche revoluta*.

annulus in otherwise $\pm$ flat central part of corolla; **lobes** 14-18 mm long, 14-18 mm broad at base, strongly folded back behind flower to give it turban-like shape, broadly ovate, acute, margins slightly recurved so that upper surface slightly convex, with purple vibratile clavate cilia 2-3 mm long all along margins. **Corona** $\pm$ 10 mm tall, 8 mm broad, raised on stout pale yellow stipe up to 2 mm long; **outer lobes** 2-3 mm long, $\pm$ 2 mm broad, ascending, often $\pm$ rectangular, obtusely bifid to tridentate or nearly

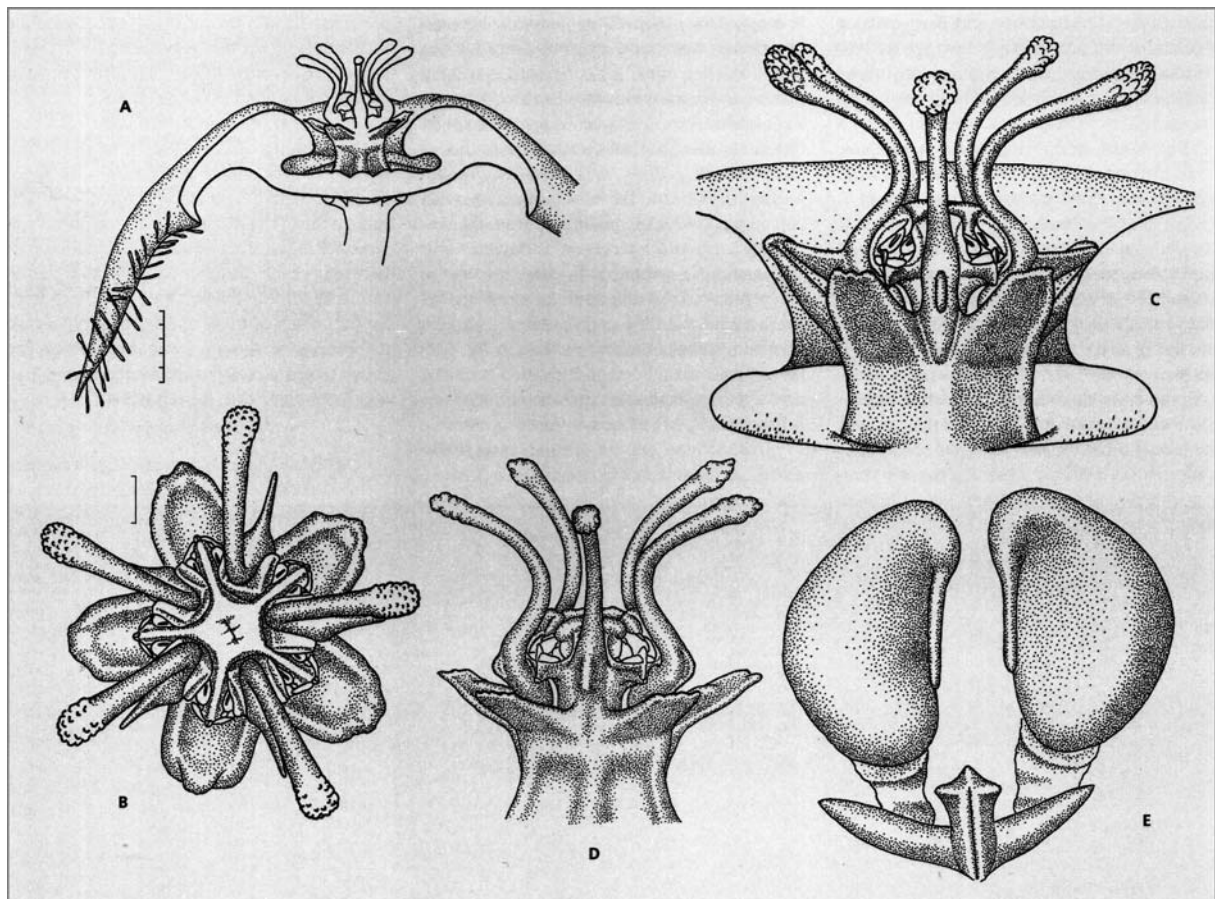


Fig. 20.3. *Tromotriche revoluta*. A, side view of dissected flower. B, face view of gynostegium. C, D, side view of gynostegium (C with centre of corolla). E, pollinarium. Scale bars: A, 5 mm; B-D, 1 mm (at B); E, 0.25 mm (at A). Drawn from: A, D, PVB 6021, Kalkgat, north of Vanrhyn's Pass; B, C, E, PVB, Beeswater, Knersvlakte.

truncate, channelled down inner surface, dark brown becoming yellow around bases; **inner lobes** 5-6 mm long, adpressed to backs of anthers then erect for short distance then recurved, dorsiventrally flattened towards base then terete and swelling into clavate-tuberculate apex, usually with spreading laterally flattened narrowly deltoid horn 1-4 mm long near base, brown to yellow speckled with purple.

Distribution and habitat

Tromotriche revoluta occurs fairly widely on the Knersvlakte of southern Namaqualand and around its margins. It is rather more common on the eastern boundaries of the Knersvlakte on the slopes of the escarpment from north-west and south of Loeriesfontein to Vanrhyn's Pass and then southwards along the valley of the Olifants River to near Clanwilliam. Along the escarpment it is found among rocks and bushes and can even be seen quite high up on steep slopes or on the summits above them. In these rather sheltered circumstances the stems are somewhat scattered but can be quite long (up to 500 mm tall) and relatively thick.

On the Knersvlakte the species is occasionally found on rocky outcrops and much more rarely in sandy areas. Here the stems are usually very widely scattered and are often only 30-50 mm, tall but a single plant may cover an area of 2-3 sq. m.

Diagnostic features and relationships

In *T. revoluta* many of the stems in a clump have a distinctly rhizomatous tendency, forming slender, cylindrical runners (usually less than 10 mm thick) which spread horizontally beneath the surface of the soil for up to 1 m or more. When they rise and emerge from the soil, they become erect, thicker and conspicuously 4-angled and then they have the characteristic pale grey-green colour of this species.

The inside of the flower in *T. revoluta* is strongly convex, with the lobes folded back behind the centre, giving the whole flower a turban-like shape. It is very variable in colour, but is usually red-brown on the lobes, becoming steadily paler towards the centre where it is a striking, ivory-like cream on the annulus and in the tube. In the centre of the flower there is a small but significant corolla tube enclosing the corona at least to the level of the anthers. The mouth is constricted by a thick overhanging ledge of tissue from the relatively massive annulus and below this ledge the tube widens out to a broader, flat base. If the outside of the flower is examined, it will be seen that it is nearly entirely flat behind the tube, so the tube itself is almost completely created by the massively thickened annulus. On the inside the flower is quite shiny and the surface is smooth except for some small papillae in the flat basal portion of the tube.



Fig. 20.4. *T. revoluta*, PVB 6021, Kalkgat, north of Vanrhyn's Pass.

The corona is raised in the centre on a stout pentagonal stipe and has comparatively short, dark outer lobes which spread towards the sides of the tube. The inner lobes rise towards the centre and then diverge, eventually ending with slender but swollen, clavate and tuberculate apices. Each one has a small, laterally flattened dorsal horn near its base, though this may be absent in some plants.

Within *Tromotriche*, *T. revoluta* is unmistakable on account of its relatively thick, square stems with more than usually prominent angles and the especially large flowers with their thick annulus.

History

Tromotriche revoluta was discovered by Francis Masson on dry plains under bushes in the Karoo beyond 'the North Olifants River' (Masson 1796-8). This seems to suggest that he collected it on the Knersvlakte and it was probably found in late October or early November 1774 when he was in that area with Thunberg.



Fig. 20.5. *T. revoluta*, PVB 6835, north of Nieuwoudtville.

2. *Tromotriche thudichumii*

Tromotriche thudichumii (Pillans) L.C. Leach, J. S.

African Bot. 48: 426 (1982).

Stapelia thudichumii Pillans, *J. S. African Bot.* 25: 375 (1959).

Type: South Africa, Cape, Uitkomst, Tanqua Karoo, *Thudichum* sub BOL 26740 (BOL).

Few-stemmed to dump-forming small succulent up to 150 mm diam., sometimes forming patches up to 0.5 m diam. of scattered stems. **Stems** above-ground 20-100 (-200) mm long, 8-15 mm thick, decumbent, often spreading horizontally underground for up to 0.25 m then erect, usually brownish green; **tubercles** 1-2 mm long, obscure, joined into 4 (-6) obscure and very obtuse angles along stem so that stem almost cylindrical, each tipped with small deltoid tooth (< 1 mm long) flanked by 2 minute stipular denticles. **Inflorescences** 1-6, randomly distributed along stem, each bearing 1 (-2) flowers $\pm$ without peduncle and with 1 or more deltoid acute bracts $\pm$ 1 mm long at base; **pedicel** 6-15 mm long, 1.0-1.5 mm thick, spreading and holding flower facing $\pm$ horizontally; **sepals** (3-) 5-8 mm long, < 1.5 mm broad at base, lanceolate, acute. **Corolla** 20-30 mm diam., $\pm$ rotate-reflexed; outside green to brownish with 3 purplish veins on each lobe; inside shiny red-brown changing to greenish towards tips of lobes and pale yellow in tube, all over (tube to edges of lobes) with small clavate to spherical or cylindrical papillae; **tube** 1.0-2.5 mm long, 6 mm broad, pentagonal, shallowly bowl-shaped, formed entirely by thickening of corolla into low annulus below bases of lobes in otherwise $\pm$ flat central part; **lobes** 8-10 mm long, 10-13 mm broad at base, strongly reflexed to wrap around stem, broadly ovate-deltate, acute, margins somewhat folded back, with vibratile purple to white clavate cilia 1-2 mm long all along margins (longest near bases of lobes). **Corona** $\pm$ 5 mm tall, 6-8 mm broad, raised on relatively slender pale yellow cylindrical stipe $\pm$ 1 mm long; **outer lobes** 2.0-2.5



Fig. 20.6. *T. revoluta*, PVB 6021, Kalkgat, north of Vanrhyn's Pass.

TROMOTRICHE THUDICHUMII

mm long, ascending-spreading, $\pm$ rectangular, truncate to bifid at apex, usually channelled down inner surface, dark brown becoming yellow towards base; **inner lobes** $\pm$ 2 mm long, adpressed to backs of anthers and ascending in column to crossing over in centre, dorsiventrally flattened near base then terete and swelling slightly into clavate-tuberculate apex, with spreading laterally flattened narrowly deltoid horn 1.5–2.5 mm long at base, pale to dark brown becoming yellow towards base.

Distribution and habitat

Tromotriche thudichumii is found over much of the Ceres Karoo, but it does not seem to occur in the extreme south and east or in the very arid region in the middle around the Tanqua River where few perennials (other than the occasional reckless *Hoodia*) dare to establish themselves. However, it is not endemic to the Ceres Karoo, as was previously thought to be the case (Leach 1984b); I have found it in the high area north of Middelpos and on the plateau south-west of Calvinia.

Specimens of *T. thudichumii* usually grow in flat, sometimes gravelly areas, often in association with various spiny and non-spiny gregarious species of *Ruschia*. It is sometimes also found among dolerite rocks at the foot of or on the slopes of hills and it is the only species of *Tromotriche* that shows any tolerance for soils partly derived from dolerite.

Diagnostic features and relationships

Tromotriche thudichumii is, like *T. revoluta*, a very rhizomatous species. The stems are, however, a different and much darker, dull and usually brownish green colour. They are also not smooth, having a finely sandpapery texture which is caused by a covering of papillae much larger than those in *T. revoluta* (Bruyns 1995a). The angles are rounded, with obscure, low and very obtuse tubercles, and in this respect *T. thudichumii* closely resembles the species from Namaqualand (i.e. *T. pedunculata* and allies). From these, however, it differs most markedly in its rhizomatous habit, rather darker colour and rougher texture and the presence of a small tooth on each tubercle which is subtended by two minute, stipular denticles.

In this species the flowers are produced randomly along the stems but they appear most frequently towards the apices. There are mostly several small inflorescences on each flowering stem, but each of them usually bears only a single flower. The flower is comparatively small and is borne on a short pedicel. The lobes fold backwards but, because of the shortness of the pedicel, are not able to curl up behind the flower (as in *T. revoluta*) but rather fold back onto the stem and partly wrap around it. I have not seen much variation in the colour of the inside of the flower, it being invariably a shiny red-brown that becomes dirty greenish towards the tips of the lobes. The flowers are

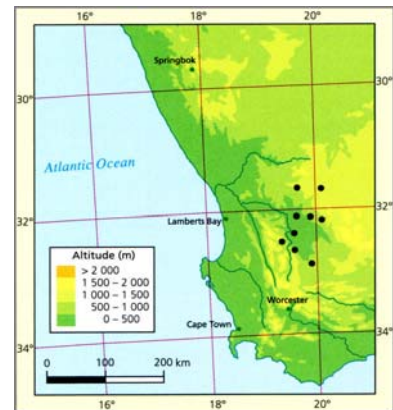


Fig. 20.7. Distribution of *Tromotriche thudichumii*.

then not particularly pretty and they also emit a slight, putrid smell. Since the lobes fold back, the centre of the flower is pushed outwards to be more exposed. This centre consists of a massively thickened, though not very prominent annulus that gives rise to a shallow tube. The inside of the tube is pale yellow and it has steep, though short sides and a relatively broad, flat base. Although the inside is comparatively shiny, it has fine papillae scattered all over it.

In the centre of the flat base of the tube, the corona stands on a comparatively long, pale yellow stipe. The more or less rectangular,

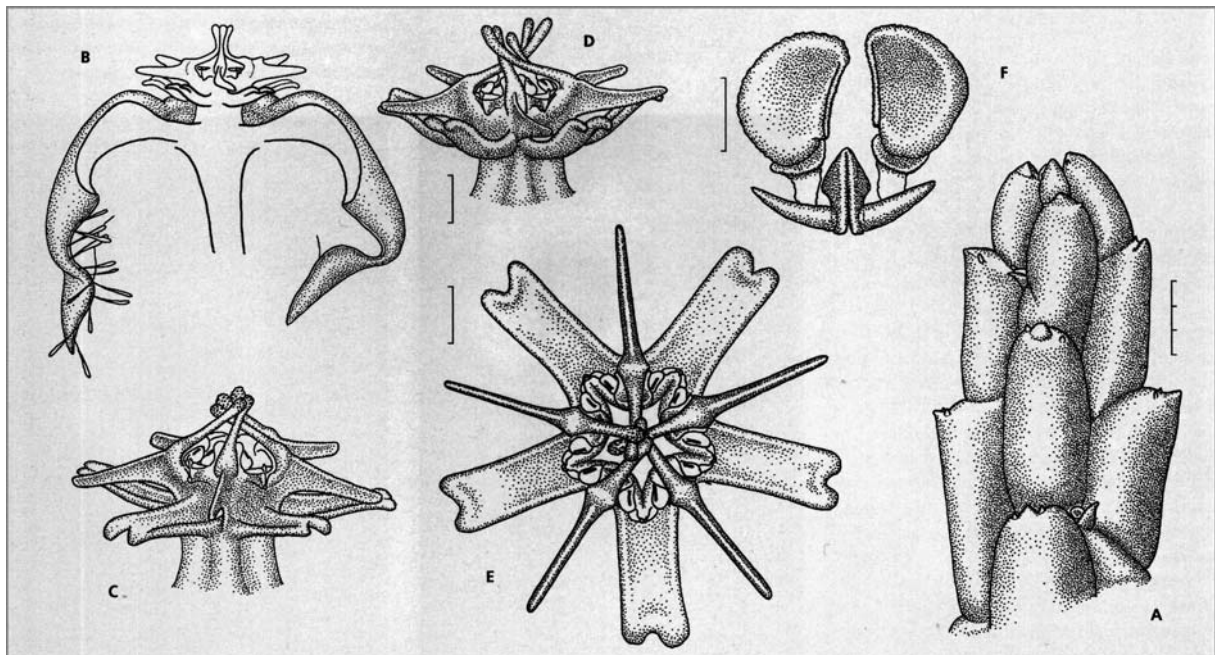


Fig. 20.8. *Tromotriche thudichumii*. A, apex of stem. B, side view of dissected flower. C, D, side view of gynostegium. E, face view of gynostegium. F, pollinarium. Scale bars: A, B, 3 mm (at A); C, D, 1 mm (at D); E, 1 mm; F, 0.25 mm. Drawn from: A, C, E, F, PVB, 30 km north of Karooport; B, D, PVB 6065, south-west of Calvinia.

spreading outer corona lobes are not unusual for this genus. However, the inner corona is most peculiar and deserves comment. The lobes are slender and relatively short, becoming cylindrical and somewhat clavate towards their tips. They spread obliquely towards the centre of the flower, where they either rise in the centre in a small column or overlap in a cluster. Each lobe has a comparatively long, laterally flattened dorsal horn which is usually about the same length as the lobe itself. This dorsal horn spreads slightly downwards nearly to the level of the outer lobes and thus it and the inner lobe form a more or less straight line.

History

Tromotriche thudichumii was first recorded by Schmidt in 1937 (PRE records) and soon afterwards, in January 1940, it was gathered again by Martinus L. Malherbe, who deposited a specimen at BOL. Many collections exist from this time, including several by Charles T. Villett (one made as early as 1940) and he made a painting of the species (BOL records) and gave it the manuscript name *Stapelia malherbei*. While Jacques Thudichum was curator of the Karoo Botanic Garden, he found that there were several stapeliads in cultivation at the garden which he could not place under any of the known names and *T. thudichumii* was one of these. He approached Carl Lückhoff with it but found that he had no further interest in the stapeliads. N.S. Pillans, who was then at the Bolus Herbarium of the University of Cape Town, was also approached with it but was at first disinclined



Fig. 20.9. *T. thudichumii*, PVB 4024, north of Karooport, Ceres Karoo. Flower with corolla lobes not yet reflexed.

to get involved, having also apparently lost interest in the stapeliads. R.A. Dyer, then at Pretoria, was also approached by Thudichum with *T. thudichumii* and some other species. After long delays Dyer wrote to Thudichum and declared that apart from the 'smaller, less elongated and not tuberculate' inner corona lobes, 'the flower is to all intents and purposes identical with that of *Stapelia revoluta*' and he was unable to give it more than 'varietal rank' (NBG archives). Thudichum seems to have remained sufficiently unconvinced of the truth of this that he later approached E.A. Schelpe, also of the Bolus Herbarium, with it. Schelpe somehow persuaded Pillans to change his mind and do something towards describing this quite obviously distinct species and eventually in 1959 Pillans described it as *Stapelia thudichumii*.



Fig. 20.10. *T. thudichumii*, PVB 4277, west of Gannaga Pass, Ceres Karoo, in habitat, May 1990.



Fig. 20.11. *T. thudichumii*, PVB 4024, north of Karooport, Ceres Karoo.

3. *Tromotriche pedunculata*

Tromotriche pedunculata (Masson) Bruyns., S. African J. Bot. 61: 208 (1995).
Stapelia pedunculata Masson, Stap. Nov.: 17, t. 21 (1797).
Caruncularia pedunculata (Masson) Haw., Syn. Pi. Succ: 333 (1812).
Tridentea pedunculata (Masson) L.C. Leach, Trans. Rhod. Scient. Assoc. 59: 4 (1978).
Type: South Africa, Cape, Khamiesberg, Masson (missing).
Lectotype: Masson, Stap. Nov.: t. 21.

Compact clump-forming succulent up to 300 mm diam. **Stems** 40-100 mm (-0.3 m) long, 10-15 mm thick, erect to nearly prostrate with ascending tips, tapering slightly towards apex, pale green to reddish; **tubercles** very obscure, so stem obscurely and very obtusely 4-angled to almost cylindrical, without apical tooth. **Inflorescences** 1-2 per stem arising mainly towards base, each bearing 5-10 flowers developing in gradual succession on peduncle 5-10 mm long; **pedicel** (30-) 45-190 mm long, 1.5-4.0 mm thick (narrowing towards base of flower), erect to prostrate (then with upturned apex holding flower facing upwards); **sepals** 4-6 mm long, 1.5 mm broad at base, narrowly deltoid, acute. **Corolla** 30-70 mm diam., rotate, deeply lobed; outside pale green with darker slightly impressed veins; inside olive-green or yellow-brown to maroon on upper two-thirds of lobes, below this whitish finely flecked with maroon and becoming darker towards gynostegium, smooth to obscurely longitudinally rugulose towards tips of lobes, finely reticulately rugulose in pale area around gynostegium and with dense crust of small nearly spherical to elongated clavate papillae around mouth of tube; **tube** $\pm$ 2 mm deep, pentagonal, formed by abrupt annular thickening near base of otherwise $\pm$ flat corolla, with mouth somewhat closed around gynostegium by overhanging ledge from annulus; **lobes** 17-30 mm long, 11-16 mm broad at base, ascending to spreading, narrowly ovate and much narrowed by strongly recurved margins, acute, with dense patch of dark purple clavate

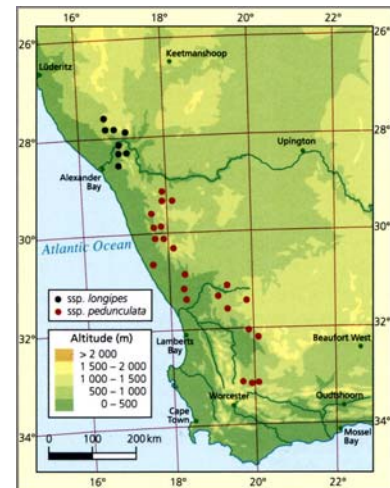


Fig. 20.12. Distribution of *Tromotriche pedunculata*.

TROMOTRICHE PEDUNCULATA

to filiform-attenuate vibratile cilia up to 2.5 mm long along margins near base. **Corona** $\pm$ 7 mm tall, 10-11 mm broad, mostly shiny purplish black, raised on short very stout stipe; **outer lobes** $\pm$ 2 mm long, ascending, $\pm$ rectangular, with truncate to subacute often crenulate apex, channelled down upper surface, often pale brown; **inner lobes** 5-6 mm long, adpressed to backs of anthers in lower half of anthers, then erect and slightly connivent, diverging towards apices, dorsiventrally flattened for lower 1-2 mm then swelling to markedly clavate irregularly and obtusely prominently tuberculate or rugulose apex, with nearly identical (except laterally flattened towards base and generally somewhat stouter and slightly longer) ascending then recurving clavate dorsal horn arising near base, lobe sometimes somewhat paler than dorsal horn.

Among all the species of *Tromotriche*, *T. pedunculata* is by far the most widespread. It is found from Witpütz in southern Namibia more or less throughout Namaqualand as far south as Vanrhynsdorp and it continues sporadically further southwards in the Ceres Karoo to near Karooport.

The flowers in *T. pedunculata* are borne on pedicels of extremely variable length which may reach 190 mm long on occasion. They are variable, too, in their habit. Sometimes they are erect and hold the flower facing upwards and sometimes they are pressed to the ground with the flower still facing upwards.

In this very variable species the corolla is relatively large, with long lobes which divide it almost to the centre. When fully open it is more or less flat inside. The lobes are very variably coloured inside, from yellowish to maroon towards the tips, changing quite suddenly near the bases of the lobes to whitish finely flecked with maroon, the maroon lying in the base of the small, shallow pits which cover the whole surface. Towards the base, the lobes are fringed with a dense beard of dark cilia. The very small tube in the centre is formed by an annular, usually very strongly pentagonal swelling in the corolla which is rather hidden behind the corona. The colour in this tube is much darker than on the corolla outside it, this darkness being somewhat accentuated by a crust of fine, spherical to clavate and darkly-coloured papillae which cover the surface.

The quite large and very ornate corona is blackish and somewhat shiny. It has tiny, channelled outer lobes that are pressed to the surface of the flower and are more or less entirely hidden from view by the inner lobes. The main and most conspicuous structures here are the shiny inner lobes and their nearly identical dorsal projections. Both the lobes and their dorsal projections are thickened towards their tips where they are densely and obtusely (i.e. not sharply) tuberculate. These structures restrict enormously the access to the pollinia and guide-rails, though not to the extent that is found in *T. baylissii* and *T. choanantha*.

3a. *Tromotriche pedunculata* subsp. *pedunculata*

Caruncularia jacquinii Sweet, *Hort. Brit.*, ed. 2: 359 (1830).

Lectotype: Jacq., Stap.: t. 60 (1806-19).

Caruncularia massonii Sweet, *Hort. Brit.*, ed. 2: 359 (1830).

Lectotype: Jacq., Stap.: t. 62 (1806-19).

Caruncularia penduliflora Sweet, *Hort. Brit.*, ed. 2: 359 (1830).

Stapelia penduliflora (Sweet) Steud., *Nomencl. Bot.*, ed. 2, 2: 631 (1841).

Lectotype: Jacq., Stap.: t. 61 (1806-19).

Caruncularia simsii Sweet, *Hort. Brit.*, ed. 2: 358 (1830).

Lectotype: Jacq., Stap.: t. 63 (1806-19).



Fig. 20.13. *T. pedunculata* subsp. *pedunculata*, PVB 8258, north of Komaggas, in habitat, August 2000.



Fig. 20.14. *T. pedunculata* subsp. *pedunculata*, PVB 5203, north of Concordia.

Stapelia laevis Decne. in DC, *Prodr.* 8: 658 (1844).
Lectotype: Bot Mag. 21: t. 793 (1804).

Corolla inside purple-brown to yellow-brown or olive-green on lobes changing near bases of lobes to white with red-brown mottling, $\pm$ smooth to finely rugulose on most of lobes, becoming reticulately rugulose near bases of lobes and below them; **lobes** with margins strongly revolute, marginal cilia clavate.

Distribution and habitat

Subsp. *pedunculata* is very much more widely distributed than subsp. *longipes*. It is found on the coastal plain from south of Port Nolloth to near Vanrhynsdorp. Further inland above the escarpment it occurs from north of Steinkopf to Springbok and then rather sporadically southwards to arid areas north-east and south-east of Nieuwoudtville. It is also of very intermittent occurrence on the Ceres Karoo, from the foot of Gannaga Pass southwards to near Karoo Poort and Patatsrivier.

Plants of subsp. *pedunculata* are often associated with the gregarious *Ruschia spinosa*. They mostly occur on firm soils, sometimes in gravelly areas but very rarely in soft ground or sand.

Diagnostic features and relationships

Leach (1980a) carefully considered the differences between his *Tridentea pedunculata* and *T. longipes* and found three of them to be most reliable and important.

Firstly, he found that in subsp. *pedunculata* the uniformly coloured part of the corolla lobes is usually only rather faintly rugulose to almost smooth. However, this is not always true and in the Ceres Karoo some plants have been seen where the lobes are quite densely and deeply rugulose (e.g. fig. 20.16), though still not to the extent usually found in subsp. *longipes*.



Fig. 20.15. *T. pedunculata* subsp. *pedunculata*, PVB 1388, Eenriet, north of Steinkopf.

Key to the subspecies of *T. pedunculata*

- | | |
|---|-------------------------------|
| Corolla inside smooth to finely rugulose on lobes, margins of lobes strongly revolute | 3a. subsp. <i>pedunculata</i> |
| Corolla inside reticulately rugulose on lobes, margins of lobes only weakly revolute | 3b. subsp. <i>longipes</i> |

Then he noted that the corolla lobes usually have the margins more tightly folded back in subsp. *pedunculata*, making the lobes more strongly convex above.

Finally, he found differences in the vibratile cilia, which occur in small dense bunches near the bases of the lobes. He described them as 'fusiform' in subsp. *longipes* and 'clavate' in subsp. *pedunculata*. However, in the specimens I have seen, I have not been very successful in observing these differences. This seems to me an excessive case of 'splitting cilia' and not worth making a fuss about.

These differences are all rather weak and

unreliable and of an entirely different order to those among the other species of *Tromotriche*. As a consequence the former *T. longipes* is reduced to a subspecies of *T. pedunculata* as we have here.

History

Subsp. *pedunculata* was discovered by Francis Masson near the Kamiesberg before 1792, for it flowered in his garden in Cape Town in 1792 and it is probable that it was collected on the same expedition on which he found *T. aperta*.

3b. *Tromotriche pedunculata* subsp. *longipes*

Tromotriche pedunculata subsp. *longipes*

(C.A.Luckh.) Bruyns, *comb. et stat. nov.*

Stapelia longipes C.A.Luckh., *S. African Gard. & Country Life* 24: 245 (1934).

Tridentea longipes (C.A.Luckh.) L.C.Leach, *Excelsa Taxon. Ser.* 2: 43 (1980).

Tromotriche longipes (C.A.Luckh.) Bruyns, *S. African J. Bot.* 61: 208 (1995).

Type: Namibia, Witpütz, E. J. Rusch sub *Lückhoff* 194 (missing).

Neotype: E. J. Rusch sub *BOL* 31684 (BOL).

Stapelia longipes var. *namaquensis* C.A.Lückh. in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1145 (1937).

Type: South Africa, Swartwater, Van Heerde sub *Lückhoff* 217 (missing).

Lectotype (selected here): White & Sloane, *Stap.*, ed. 2, 2: fig. 617.

Corolla inside dark maroon or brown on lobes changing abruptly near bases of lobes to white on rugosities with maroon or brown between them, reticulately rugulose; **lobes** with margins far less revolute than in subsp. *pedunculata*, marginal cilia fusiform attenuate and usually acute.

Distribution and habitat

Subsp. *longipes* is found from Witpütz in southern Namibia to near Port Nolloth in Namaqualand. It is mainly confined to the lower slopes of the hills and mountains facing the coastal plains. Nevertheless, in South Africa some collections have been made as far east as Eksteenfontein and on the Rosyntjie Mountain, while in Namibia it has been found in some of



Fig. 20.16. *T. pedunculata* subsp. *pedunculata*, PVB 6266, south-east of Karooport, Ceres Karoo.

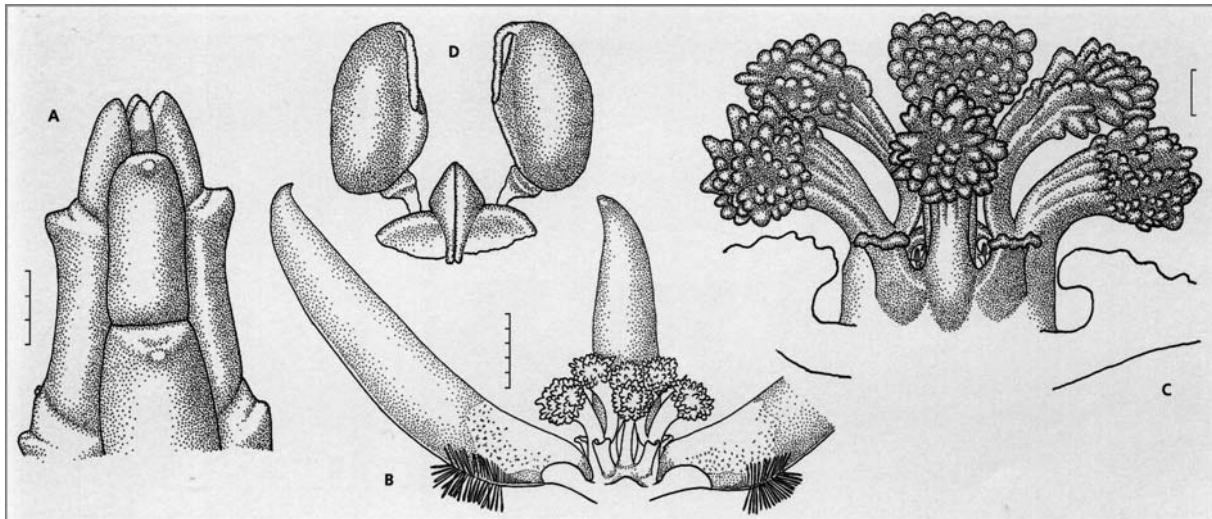


Fig. 20.17. *Tromotriche pedunculata* (C. subsp. *longipes*; rest subsp. *pedunculata*). A, apex of stem. B, side view of dissected flower. C, side view of centre of dissected flower with 'annulus'. D, pollinarium. Scale bars: A, 3 mm; B, 5 mm; C, 1 mm; D, 0.25 mm (at A). Drawn from: A, D, PVB 1388, Eenriet, north of Steinkopf; B, PVB 5203, north of Concordia; C, PVB 3184, Namuskluft, east of Rosh Pinah, Namibia.

TROMOTRICHE RUSCHIANA



Fig. 20.18. *T. pedunculata* subsp. *longipes*, PVB 3184, Namuskluft, east of Rosh Pinah, Namibia.



Fig. 20.19. *T. pedunculata* subsp. *longipes*, PVB 8838, east of Lorelei, Namibia, in habitat, September 2000.

the valleys running towards the Orange River east of Lorelei.

Specimens invariably grow on gentle, gravelly slopes or occasionally in loamy soils in valleys. Many of them grow in the open among small bushes or stones but they will also be found sheltering under shrubs such as robust forms of *Euphorbia rhombifolia* and *Zygophyllum*. Subsp. *longipes* may also be found in patches of quartz gravel.

Diagnostic features and relationships

Plants of this subspecies are often quite compact with relatively short, erect stems but, if they are well sheltered, the stems may sprawl on the ground with only the tips ascending and under such circumstances they have been seen to grow up to 0.3 m long.

The pedicel in subsp. *longipes* is remarkably variable in length and Leach (1980a) noted that it could be prostrate or erect. After fertilisation the pedicel becomes slightly stouter and erect

once the follicles begin to grow, so mature follicles are held well above the ground.

In subsp. *longipes* the pitting of the inner surface of the corolla is accentuated into irregular transverse rugulosities and the colour is generally a more intense maroon or brown than one finds in subsp. *pedunculata*. Other differences from subsp. *pedunculata* are discussed above.

History

Subsp. *longipes* appears to have been discovered in 1925 by Rudolf Marloth at Kubus in the Richtersveld. The material from which Carl Lückhoff described '*Stapelia longipes*' was sent to Kirstenbosch by Ernst Julius Rusch in November 1932. These plants proved tricky to cultivate and it was only in 1934 that Lückhoff was given more material from the same place by David Pringle of Port Elizabeth. This was in flower and so a description could be drawn up.



Fig. 20.20. *T. pedunculata* subsp. *longipes*, PVB 8838, east of Lorelei, Namibia, in habitat, September 2000.

4. *Tromotriche ruschiana*

Tromotriche ruschiana (Dinter) Bruyns, S. African J. Bot. 61:208(1995).

Stapelia ruschiana Dinter, Feddes Rept. Spec. Nov. Regni Veg. 19:177 (1923).

Tridentea ruschiana (Dinter) L.C.Leach, Trans. Rhod. Scient. Assoc. 59: 4 (1978).

Type: Namibia, Klinghardt Mountains, Dinter 3963 (missing).

Neotype: Klinghardt Mountains, Plowes 4988 (PRE).

Compact to somewhat spreading clump-forming succulent up to 300 mm diam. **Stems** 40-200 mm long, 6-20 mm thick, erect to spreading or rhizomatous, tapering slightly towards apex, pale green to reddish; **tubercles** very obscure so stem very obscurely 4-angled to almost cylindrical, without apical tooth. **Inflorescences** 1-2 per stem arising mainly towards base, each bearing 1-2 flowers developing in gradual succession on sometimes branching peduncle 5-40 mm long and 6 mm thick; **pedicels** 40-60 mm long, 2-4 mm thick, spreading with upturned apex holding flower facing upwards; **sepals** 2-5 mm long, 1.5-2.0 mm broad at base, narrowly ovate to deltate, acute, sometimes with few short marginal cilia. **Corolla** (30-) 40-50 mm diam., shallowly campanulate; outside pale green with reddish spots, becoming green on lobes; inside red-brown to dark maroon on lobes changing $\pm$ abruptly to white on rugosities with dark red between them in lower third of lobes and in tube, rugulose over whole surface, often also with 3 longitudinal grooves on lobes running into tube, in lower 5 mm of tube with erect stout clavate to cylindrical papillae $\pm$ 0.25 mm long, sometimes extending as cilia below sinuses of lobes; **tube** 8-10 mm long, 10-12 mm broad, cupular, pentagonal, containing whole gynostegium; **lobes** 14-25 mm long, 6-10 mm broad at base, spreading to somewhat recurved, convex from recurved margins, with clavate to fusiform-attenuate vibratile cilia 1.5-3.0 mm long along margins of lower third. **Corona** $\pm$ 6-8 mm tall, 8 mm broad, raised on short

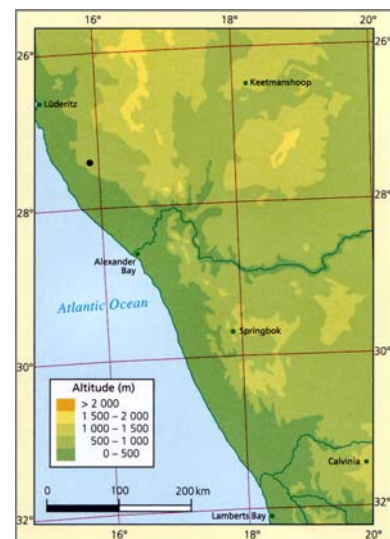


Fig. 20.21. Distribution of *Tromotriche ruschiana*.

thick pale red stipe; **outer lobes** 2-3 mm long, 1.5 mm broad, ascending, $\pm$ rectangular, crenulate towards obtuse to acute apex, channelled down upper surface, yellow to purple-brown; **inner lobes** $\pm$ 5 mm long, adpressed to backs of anthers in lower half of anthers, then erect and slightly connivent, diverging towards apices, dorsiventrally flattened for lower 1-2 mm then swelling to clavate obscurely tuberculate apex, shiny purplish black, with nearly identical (except laterally flattened towards base and generally somewhat stouter) ascending then recurving clavate dorsal horn arising near base, lobe sometimes somewhat paler than dorsal horn.

Distribution and habitat

Tromotriche ruschiana is one of the most localised species of stapeliad in southern Africa and, as far as is known, it is restricted to the hills which make up the Klinghardt Mountains. These are situated about 100 km south-east of Lüderitz in the so-called *Sperrgebiet* in the south-western corner of Namibia.

Plants are found on rocky slopes of hills, often with a considerable amount of reddish, wind-blown sand filling up the crevices among the rocks and partly covering the stems.

Diagnostic features and relationships

In *T. ruschiana*, plants may form clumps up to 300 mm in diameter but they also often have several stems spreading beneath stones away from the main clump for a distance of up to 200 mm, after which they rise to the surface once more. In cultivation they tend, very readily, to spread out horizontally and become almost creeping or slightly rhizomatous. The stems are even more rounded than is usual for *T. pedunculata* but are otherwise very similar to them in appearance.



Fig. 20.22. *T. ruschiana*, PVB 7900, Klinghardt Mountains, south of Lüderitz, Namibia.

Although it shares many features of size, shape and colouring with the flower of *T. aperta*, the flower of *T. ruschiana* is more similar to that of *T. pedunculata* and the colour scheme of the corolla in particular is similar to that of subsp. *longipes*. As in the case of *T. aperta*, when the flower of *T. ruschiana* is fully open, there is a cupular tube in the centre which is considerably deeper than the height of the gynostegium. This also provides the most obvious difference from *T. pedunculata*, where there is no noticeable tube. As in many of these species, in *T. ruschiana* there is a crust of dark clavate papillae in the tube in its lower half and these are often comparatively long and are more slender than in *T. pedunculata*. As in *T. pedunculata* but unlike *T. aperta*, the margins of the corolla lobes are adorned with a small patch of vibratile cilia near their base, around the position where the colour of the lobes changes.

The outer corona lobes are pressed into grooves towards the base of the tube and are relatively pale, with rather irregularly thickened

ends which often become moist with the secretion of nectar. They have a deep groove down their middle. The inner lobes are more slender than those in *T. pedunculata*. In both species the inner lobes and their dorsal projections have clavate apices. Whereas in *T. pedunculata* these apices are deeply and coarsely tuberculate, in *T. ruschiana* they are faintly pitted but are otherwise nearly entirely smooth and consequently they are far more shiny. As the inner corona lobes are more slender, the pollinia are more accessible in *T. ruschiana* than in *T. pedunculata*.

History

Tromotriche ruschiana was first recorded in September 1922 by M. Kurt Dinter, who found it growing in stabilised sand under a shrub on the slopes of Pietab in the Klinghardt Mountains (Dinter 1923). He mentioned in his diary for 15 September that he had long held it to be a *Caralluma*, so he must have actually discovered it sometime before this.

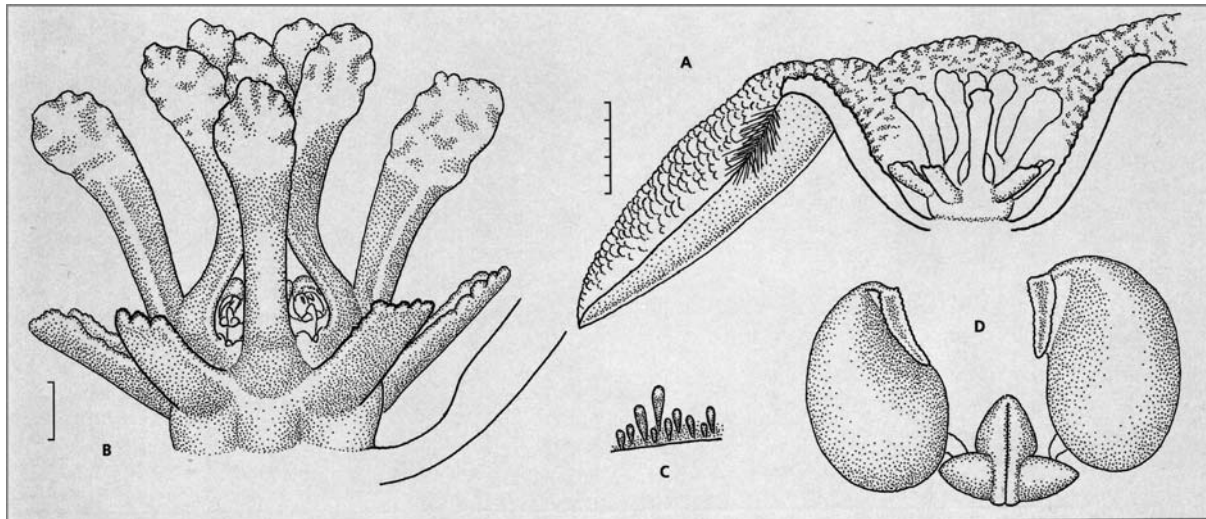


Fig. 20.23. *Tromotriche ruschiana*. A, side view of part of dissected corolla. B, side view of gynostegium. C, papillae inside corolla around mouth of tube. D, pollinarium. Scale bars: A, 5 mm; B, 1 mm; C, 0.5 mm (at A); D, 0.25 mm (at A). Drawn from: PVB 7900, Klinghardt Mountains, south of Lüderitz, Namibia.

5. *Tromotriche umdausensis*

Tromotriche umdausensis (Nel) Bruyns, S. African J. Bot. 61: 207 (1995).

Caralluma umdausensis Nel, Jahrb. Deutschen Kakt.-Ges. 3: 22 (1935).

Tridentea umdausensis (Nel) L.C. Leach, Trans. Rhod. Scient. Assoc. 59: 4 (1978).

Type: South Africa, Cape, Umdaus, *Herre* sub STE 6079 (missing).

Neotype: between Springbok and Klipfontein, *Herre* sub STE 7068 (BOL).

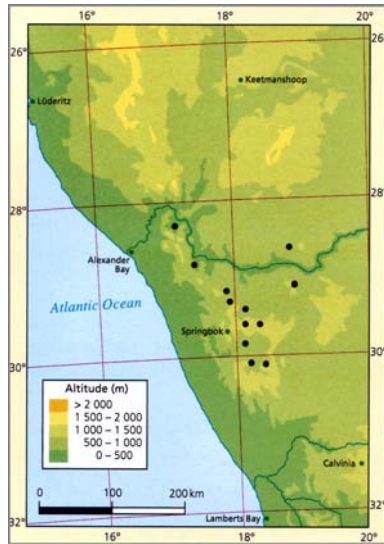


Fig. 20.25. Distribution of *Tromotriche umdausensis*.



Fig. 20.24. *T. umdausensis*, near Umdaus, north of Steinkopf, in habitat, December 1976.

Compact clump-forming small succulent up to 150 (-300) mm diam. **Stems** 30-100 mm long, 6-15 mm thick, erect to spreading, tapering slightly towards apex, pale green to reddish; **tubercles** very obscure so stem obscurely and very obtusely 4-angled to almost cylindrical, without apical tooth. **Inflorescences** 1-3 arising randomly on stem, each bearing 1-2 flowers developing in gradual succession on peduncle up to 5 mm long; **pedicel** 20-30 (-50) mm long, 2 mm thick, ascending then becoming horizontal at apex so that flower facing horizontally or slightly nodding; **sepals** 3-4 mm long, 1.0-1.5 mm broad at base, narrowly deltoid, acute. **Corolla** 15-30 mm diam., campanulate; outside cream to reddish with slightly darker impressed veins (5 per lobe); inside in tube usually red to brown reticulately to radially marked with white to yellow, lobes uniformly yellow to red-brown or brown and often faintly reticulately mottled and rugulose with cream or white,

shallowly rugulose in tube where rugulosity $\pm$ radially arranged, more deeply rugulose on lobes, with small nearly spherical to elongated clavate papillae towards base of tube; **tube** 5-8 mm long, 10-12 mm broad, cupular, with abrupt annular thickening around corona near base; **lobes** 9-12 mm long, 5-10 mm broad at base, ascending to spreading, ovate, acute, margins strongly folded back, ciliate. **Corona** $\pm$ 3 mm tall, 5 mm broad, purple-black to pale brown, raised on short stout stipe; **outer lobes** $\pm$ 1 mm long, ascending, fused to dorsal bases of inner lobes so as to form pouch between adjacent inner lobes, with crenulate-dentate margin and sometimes longer tooth in middle; **inner lobes** 0.7-1.0 mm long, adpressed to backs of anthers and seldom exceeding them, dorsiventrally flattened, deltoid, obtuse (acute), with obtuse dorsal gibbosity near base in series with and fused to outer lobes.

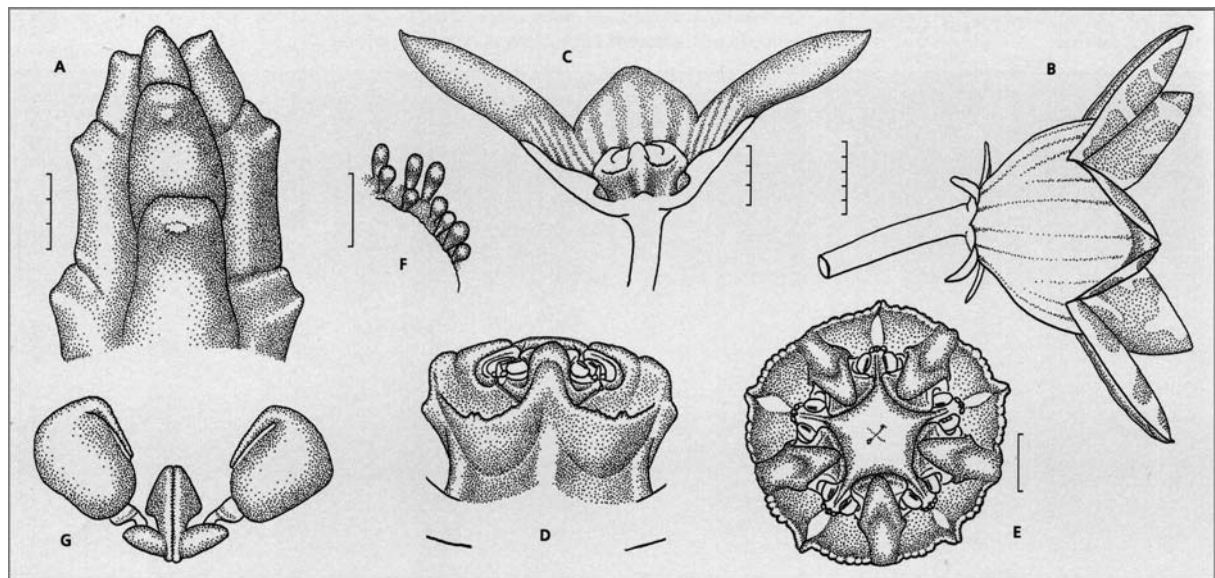


Fig. 20.26. *Tromotriche umdausensis*. A, apex of stem. B, side view of flower. C, side view of dissected flower, showing the annulus. D, side view of gynoecium. E, face view of gynoecium. F, papillae inside corolla around 'annulus'. G, pollinarium. Scale bars: A, 3 mm; B, 5 mm; C, 3 mm; D, E, 1 mm (at E); F, 0.5 mm; G, 0.25 mm (at F). Drawn from: C, PVB 6346, north-east of Kamieskroon; rest PVB 1337, Eenriet, north of Steinkopf.



Fig. 20.27. *T. umdausensis*, PVB 1341, north-east of Kamieskroon.



Fig. 20.28. *T. umdausensis*, PVB 4687, south-west of Gamooep.



Fig. 20.29. *T. umdausensis*, PVB 8245, east of Springbok.

Distribution and habitat

Tromotriche umdausensis is endemic to the very arid parts of the north-western corner of South Africa and the southernmost part of Namibia. It mainly occurs towards the eastern edge of the winter-rainfall region. It is found along the eastern flank of the escarpment, from Hellskloof to Eksteenfontein and further east to Pofadder in Bushmanland and Warmbad in south-eastern Namibia. It is extremely uncommon in the area between Pofadder and Warmbad, where it appears to be known from only two collections, one of which is the sole known record from Namibia. From the Steinkopf area, where it is more common, it continues southwards, again always on the eastern and much drier side of the Kamiesberg and reaches its southernmost limits to the north-east of Kamieskroon.

Plants are mainly found on gently sloping, quartz-strewn patches around the base of gneiss hills, occasionally growing inside bushes but often fully in the open.

Diagnostic features and relationships

Specimens of *T. umdausensis* form dense clumps of short, neatly packed, bluntly 4-angled and almost cylindrical stems which are usually small. These stems have a slight tendency to spread underground when 'in a tight corner', as sometimes happens between stones or in a pot in cultivation.

In this species the pedicel is ascending with an abruptly bent apex. Consequently the dainty flowers usually have a modest, slightly nodding habit. The corolla tube occupies about half the length of the flower with the lobes spreading at the mouth, giving the flower a distinctly campanulate shape. The flowers are extremely variable in colour, even more so than in *T. herrei*, and the lobes may be anything from plain yellow to red-brown with whitish, reticulated, slightly raised ridges. The tube is usually strikingly radially marked with white against a red or brown background. These radial markings are of somewhat irregular thickness, which creates almost the same impression as if the colour had run down the tube. The raised ridges on the corolla are neither as fine and dense as in

T. pedunculata and *T. aperta*, nor do they stand out as heavily as in *T. herrei*. The flowers emit a mild smell of bad breath or excrement. Right at the base and not visible unless the corolla is dissected, there is a small, thickened, pentagonal annulus around the corona. From the annulus to the mouth of the tube, the surface is densely encrusted with small, spherical to clavate papillae.

The outer corona in *T. umdausensis* and *T. aperta* does not consist of discrete, more or less rectangular lobes as in all other species of *Tromotriche*. Here the lobes are very short and are fused to the lower backs of the inner lobes, thereby forming a quite substantial pouch beneath each guide-rail. In total these five pouches give the entire gynostegium a pentagonal, cupular appearance and this cup is pressed into the five corners of the small annulus. Right at the base of each pouch is a small, deep orifice which appears to be lined with secretory cells and in which nectar collects to some extent. The guide-rails are remarkably short but are still quite capable of holding a pollinium until the caudicle breaks, with or without a corpuscle still in place above them.

This species is separated from all the others in *Tromotriche* by its very short inner corona lobes. As usual, these are adpressed to the backs of the anthers but mostly they do not exceed the anthers. In other words, they do not rise into any sort of column above the centre of the style-head as happens in all the other species.

History

Tromotriche umdausensis is usually considered to have been discovered north of Steinkopf by Hans Herre in September 1929, during his first expedition to the Richtersveld (White & Sloane 1937). According to the records in the Bolus Herbarium it was also collected by N.S. Pillans in 1931 and J. Archer in November 1932, in much the same area. However, among these records there is also a small but unmistakable specimen from a collection made by George G. Wrentmore in October or November 1915 near Concordia and so credit for the discovery of this species must go to him. The only known collection from Namibia was made near Warmbad by Waldemar F. Bayer in April 1939.



Fig. 20.30. *T. umdausensis*, near Umdaus, north of Steinkopf, in habitat, December 1976.

TROMOTRICHE APERTA

6. *Tromotriche aperta*

Tromotriche aperta (Masson) Bruyns, *S. African J. Bot.* 61: 208 (1995).

Stapelia aperta Masson, *Stap. Nov.*: 23, t. 37 (1797).
Orbea ? aperta (Masson) Sweet, *Hort. Brit.*, ed. 1: 277 (1826).

Caruncularia aperta (Masson) Sweet, *Hort. Brit.*, ed. 2: 359 (1830).

Caralluma aperta (Masson) N.E.Br., *Hooker's Icon. Pl.* 20: t. 1905 A (1890).

Tridentea aperta (Masson) L.C.Leach, *Trans. Rhod. Scient. Assoc.* 59: 4 (1978).

Type: South Africa, Namaqualand, near Kokfontein (Kookfontein), Masson (missing).

Lectotype: Masson, *Stap. Nov.*: t. 37.

Compact clump-forming small succulent up to 150 (-300) mm diam. **Stems** 30-100 mm long, 6-15 mm thick, erect to spreading, tapering slightly towards apex, pale green to reddish; **tubercles** very obscure so stem obscurely and very obtusely 4-angled to almost cylindrical, without apical tooth. **Inflorescences** 1-2 arising randomly on stem but mainly towards base, bearing 1-2 flowers developing in gradual succession on stout peduncle up to 5 mm long; **pedicel** 60-140 mm long, 2-3 mm thick, mostly prostrate with upturned apex holding flower facing upwards; **sepals** 3-5 mm long, 1.5 mm broad at base, narrowly deltoid, acute. **Corolla** 30-40 mm diam., shallowly campanulate; outside pale green spotted with maroon; inside with dark red-brown patch around corona changing to white on rugosities with red-brown in between them on most of tube and at least on bases of lobes, then usually uniformly beige or brown or red-brown for rest of lobes, reticulately rugulose all over except towards base of tube, with small nearly spherical to elongated clavate papillae around

corona; **tube** 5-8 mm deep, pentagonal, cupular, with corolla thickened towards base and forming overhanging 'annulus' near base; **lobes** 12-25 mm long, 7-10 mm broad at base, ascending to spreading, narrowly ovate to deltate, acute, convex above from recurved margins, eciliate. **Corona** $\pm$ 6 mm tall, 5 mm broad, raised on short very stout stipe; **outer lobes** $\pm$ 1 mm long, ascending and closely adpressed to sides of tube, laterally fused to bases of inner lobes so as to form pouch between adjacent inner lobes, with crenulate-papillate and dentate margin sometimes with distinct central tooth, yellow-brown to blackish; **inner lobes** 3-4 mm long, adpressed to backs of anthers then connivent and erect in small column and slightly diverging towards apices, dorsiventrally flattened becoming slightly clavate-tuberculate towards apex, with irregularly papillate dorsal crest near base confluent with outer lobes, usually red, sometimes blackish towards tips.

Distribution and habitat

Tromotriche aperta has an essentially coastal distribution in the arid parts of south-western Namibia and the north-western Northern Cape, well within the winter-rainfall area. In Namibia it is known from the vicinity of the Aurus Mountains and the Obib Mountains, which lie to the west of Rosh Pinah. South of this there appears to be a gap in the distribution, and *T. aperta* begins to appear once more around Lekkering. From here it continues sporadically southwards to Soebatsfontein and between Wallekraal and Garies. It is found a little further east around Eksteenfontein but this seems to be the only area where it ventures off the coastal plain and away from the low, coastal hills.

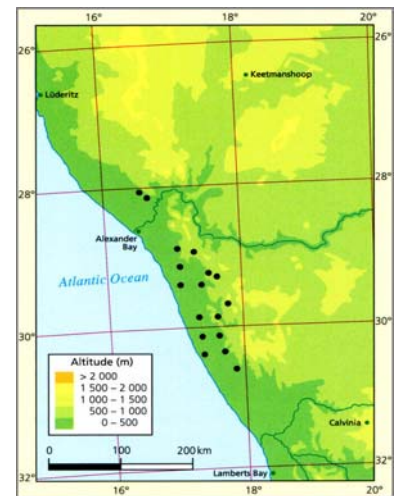


Fig. 20.31. Distribution of *Tromotriche aperta*.

Tromotriche aperta is always found in *hard-evel* or karroid areas where the ground is firm and loamy and is covered with short bushes. It does not occur in the soft sand of the *sandveld*. In a few places it has been found growing in small patches of hard ground surrounded by sand. While it does sometimes occur on flats under small bushes, it more usually grows on gentle slopes covered with fine gravel or strewn with quartz or gneiss pebbles.

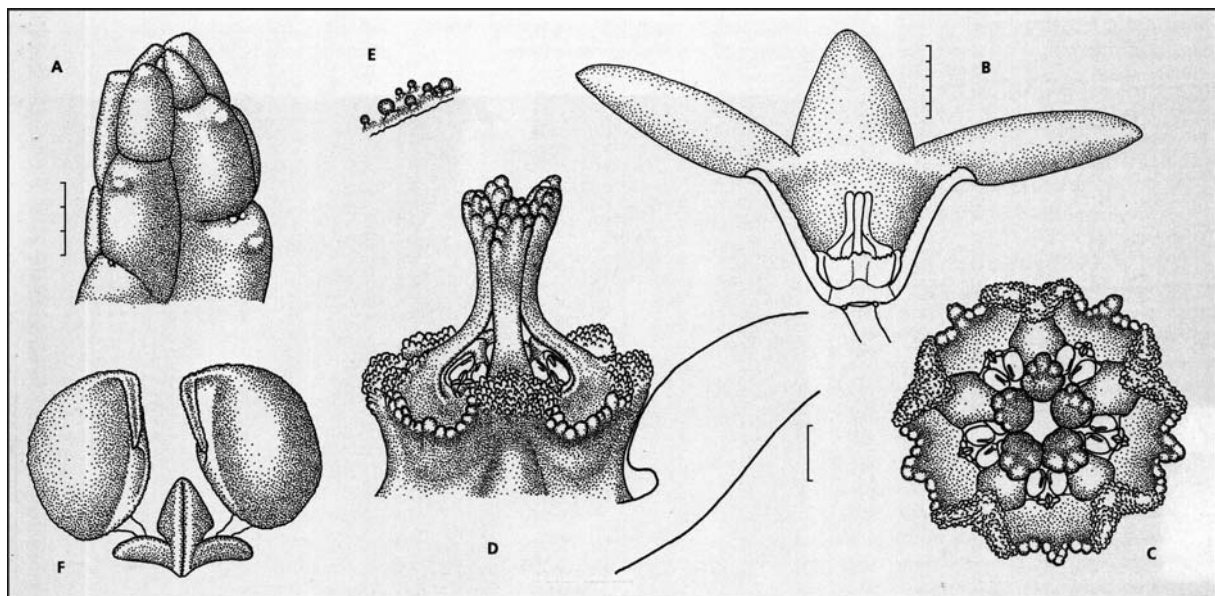


Fig. 20.32. *Tromotriche aperta*. A, apex of stem. B, side view of dissected flower. C, face view of gynostegium. D, side view of centre of dissected flower. E, papillae inside corolla in mouth of tube. F, pollinarium. Scale bars: A, 3 mm; B, 5 mm; C-D, 1 mm (at D); E, 0.5 mm (at A); F, 0.25 mm (at A). Drawn from: B, PVB 7590, west of Garies towards Wallekraal; rest Bayer 8 Bruyns 830, Klein Steenbok.

Diagnostic features and relationships

The plant in *T. aperta* is indistinguishable from that of *T. pedunculata* or *T. umdausensis* and, like the former, is not at all rhizomatous. Specimens usually form tight clumps, though the stems can be spreading if the plant is sheltered.

Flowers of this species are produced in small numbers per plant and are borne on comparatively long pedicels which spread out more or less on the surface of the soil with the flowers facing upwards. They are quite striking, though not as much so as in *T. pedunculata*. The outside is pale green sometimes boldly spotted with maroon. Inside, the flower has the same reticulately rugulose surface as in *T. pedunculata* subsp. *longipes*, and there is the same abrupt change of colour from red-brown or brown on the lobes to white mottled with red-brown nearer their bases and into the tube. As in *T. umdausensis*, the corolla is somewhat campanulate but in *T. aperta* the lobes are considerably longer than the tube, which is therefore less conspicuous. The tube is distinctly pentagonal, with the vertices lying below the middle of the lobes. The flowers emit a urine-like odour.

Although the colour scheme of the flower is similar to that of *T. pedunculata*, the respective coronas are substantially different. The outer corona is similar to that in *T. umdausensis* and forms a pouch between each pair of inner lobes, with a crenulate margin. The cupular structure that it forms nestles closely in the base of the corolla tube, fitting into grooves in the side of the tube. However, the inner lobes are more substantial than in *T. umdausensis* and rise in the centre into a column. Towards the base they are dorsiventrally flattened but higher up they become more slender, swelling again to the slightly clavate-tuberculate tips. A dorsal horn as in *T. pedunculata* is absent.

History

Tromotriche aperta was discovered by Francis Masson somewhere near the present-day farm Kookfontein, which is a little to the west of Soebatsfontein in Namaqualand. He seems to have visited Namaqualand before or during 1792 but no information on these expeditions is known since he had, in fact, been expressly forbidden by his mentor and financier Joseph Banks to leave the environs of Cape Town. Consequently he kept details of these escapades into more interesting territory to himself and information on these clandestine expeditions has never come to light.



Fig. 20.33. *T. aperta*, PVB 7590, west of Garies towards Wallekraal.



Fig. 20.34. *T. aperta*, PVB 4597, hills north of Komaggas.



Fig. 20.35. *T. aperta*, near Maerpoort, east of Port Nolloth, about to flower and in fruit, in habitat, August 2000.

TROMOTRICHE HERREI

7. *Tromotriche herrei*

Tromotriche herrei (Nel) Bruyns, *S. African J. Bot.* 61:208(1995).

Stapelia herrei Nel, *Kakteenkunde* 1933: 69 (1933).
Tridentea herrei (Nel) L.C.Leach, *Trans. Rhod. Scient. Assoc.* 59: 4 (1978).

Type: South Africa, Cape, Eksteenfontein, *Herre* sub STE 6002 (missing).

Neotype: Eksteenfontein, STE 1571 (NBG).

Stapelia tigrina Nel, *Kakteenkunde* 1933:133 (1933).
Stapelia neliana A.C.White & B.Sloane, *Stap.*, ed. 2, 2: 638 (1937), *nom. superfl.*

Type: South Africa, Hellsloof, *Herre* sub STE 6049 (missing).

Lectotype: White & Sloane, *Stap.*, ed. 2, 2: fig. 607.

Compact to somewhat diffuse clump-forming succulent up to 300 mm diam. **Stems** 40-150 mm long, 10-20 mm thick, erect, tapering slightly towards apex, pale green to reddish; **tubercles** very obscure so stem obscurely and very obtusely 4-angled to almost cylindrical, without apical tooth. **Inflorescences** 1-4 arising randomly on stem but frequently towards apex, each bearing 1-3 flowers developing in gradual succession on stout knobby peduncle up to 5 mm long; **pedicel** 15-70 mm long, 2-3 mm thick, ascending to erect holding flower facing upwards; **sepals** 4-5 mm long, 1.25-2.00 mm broad at base, narrowly deltoid, acute. **Corolla** 20-60 mm diam.,

campanulate; outside pale green often with reddish veins becoming brownish on lobes; inside white to cream on raised rugosities with brown to red or green patches between them, red in tube and usually maroon to dark maroon in base of tube around gynostegium, deeply and coarsely reticulately rugulose on lobes fading somewhat in tube but with further coarse $\pm$ concentric-pentagonal rugosities around gynostegium at base of tube, without papillae in lower part of tube; **tube** 8-15 mm long, with small pentagonal basal portion 5-8 mm diam. (where corolla much thickened) then widening to inflated shallowly urceolate portion 12-25 mm diam. in middle and narrowing slightly towards mouth to 10-22 mm; **lobes** 12-20 mm long, 8-15 mm broad at base, ascending to spreading, deltate (ovate when flattened), acute, convex from strongly recurved margins, eciliate. **Corona** $\pm$ 6 mm tall, 9 mm broad, raised on short very stout stipe, usually shiny black-red becoming reddish towards base, closely contained in basal portion of tube; **outer lobes** $\pm$ 2.5 mm long, 1.5-2.0 mm broad, ascending then spreading, channelled above, with spreading finely crenulate $\pm$ truncate apices, sometimes orange-brown; **inner lobes** 4.5-5.5 mm long, adpressed to lower half of backs of anthers, then erect and connivent, dorsiventrally flattened for lower $\pm$ 1.5 mm then swelling to stoutly clavate mostly smooth (obscurely rugulose) apex $\pm$ 1.75 mm thick, with very similar (but slightly shorter and distinctly laterally flattened) ascending clavate dorsal horn arising near base.

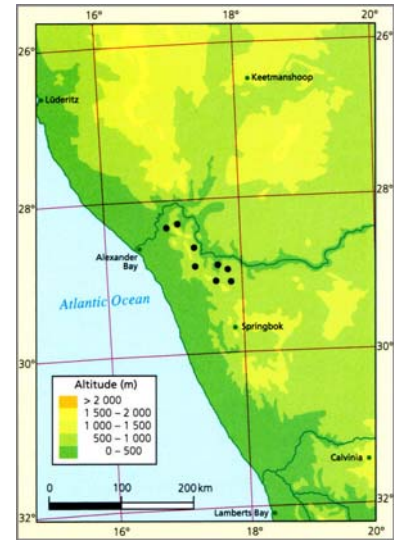


Fig. 20.36. Distribution of *Tromotriche herrei*.

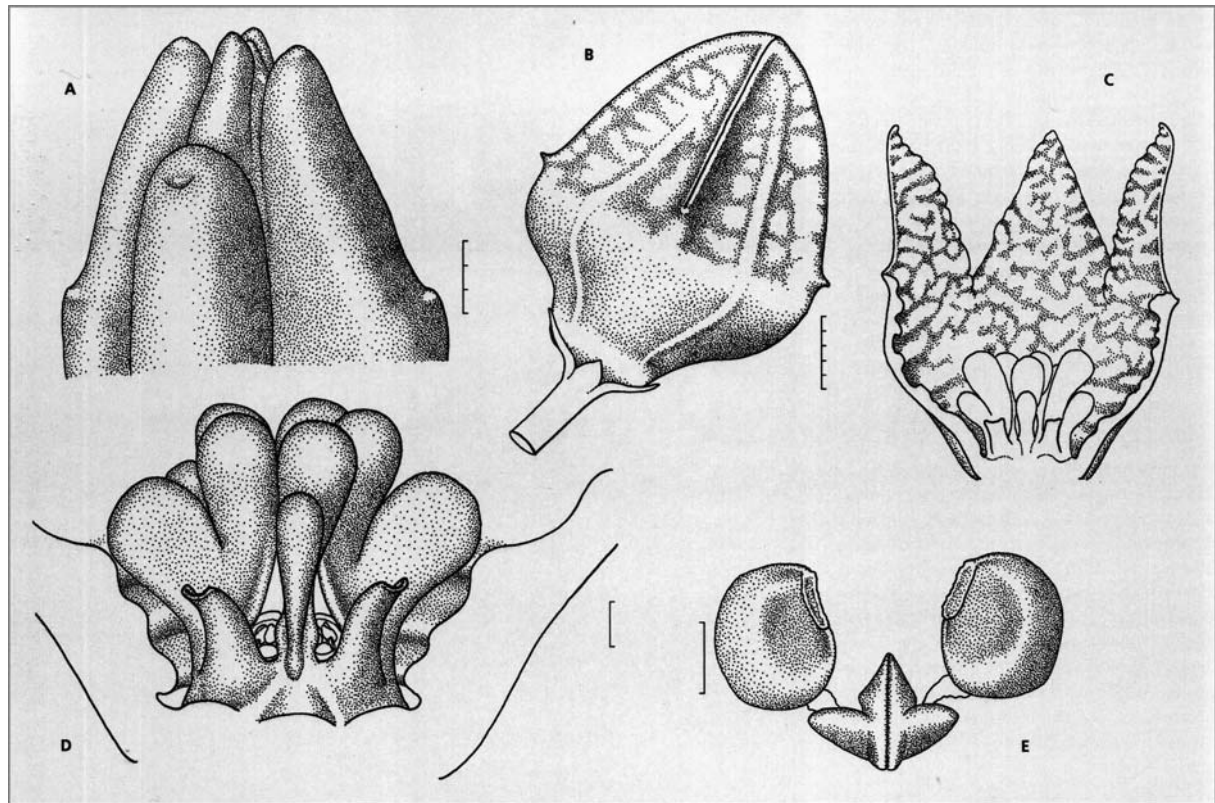


Fig. 20.37. *Tromotriche herrei*. A, apex of stem. B, bud. C, side view of dissected corolla. D, side view of centre of dissected flower showing thickened 'annulus' and gynostegium. E, pollinarium. Scale bars: A, 3 mm; B, C, 5 mm (at B); D, 1 mm; E, 0.25 mm. Drawn from: C, Heunis, Jakkalswater; rest Heunis & Bruyns 499, near Klipbok.

Distribution and habitat

Tromotriche herrei is known only in the extremely arid country on the south bank of the Orange River in the Richtersveld. Here it occurs from the vicinity of Eksteenfontein to Little Hellskloof and eastwards to the area around Jakkalswater, north-east of Steinkopf. It has also been collected a few times further west in the Hellskloof north of Kubus.

Plants of *T. herrei* are found on gentle, gneissic slopes that are usually covered with quartz gravel and invariably have an extremely scanty cover of vegetation. Although plants probably begin life under a small bush, older specimens are often (though not always) seen fully in the open among quartz or gneiss stones.

Diagnostic features and relationships

Specimens of *T. herrei* usually consist of relatively few, thick and somewhat irregularly knobby stems which may become quite tall and regularly exceed 100 mm in height. *Tromotriche herrei* often occurs with *T. umdausensis* around Jakkalswater and with *T. aperta* north of Eksteenfontein, but the comparative stoutness and irregular angles of the stems in *T. herrei* can usually be used to tell them apart.

When in flower *T. herrei* is unmistakable. The flowers are produced in small numbers

near the tips of the stems and face upwards. They consist of prominent lobes a little longer than broad and spreading from around the mouth of a comparatively deep tube. On the lobes and in the mouth of the tube the inside is covered with a network of particularly coarse, reticulate rugosities. The rugosities themselves are white and somewhat rough, rather like ridges of ice or icing sugar, and the areas between them are a darker colour which may be red or brown or even greenish. These coarse rugosities tend to become fewer in the tube and form concentric rings and then fade out lower down. If the corolla tube is examined carefully, it will be found to consist of two parts. There is a narrow portion towards the base (the 'primary' tube) which is somewhat thicker than the rest and is uniformly dark in colour. This encloses the lower part of the corona quite closely and sometimes has a small ring of tissue overhanging the slightly flattened base of the tube. This slightly flattened base is paler and thinner than the part above it and lets in light around the base of the corona to produce a window-like effect. Above the basal portion the corolla tube widens and is thinner-walled but it is constricted again somewhat at its mouth (this forms the 'secondary' tube) so that as a whole it is urceolate. The flowers have a faint excrement-like odour.

As is often the case in *Tromotriche*, the channelled outer lobes are small and insignificant



Fig. 20.38. *T. herrei*, a medium-sized plant growing entirely in the open in a patch of quartz-gravel near Jakkalswater, in habitat, August 2000.

nificant and are completely dwarfed by the comparatively massive inner lobes. They secrete nectar in noticeable quantities on their upper surface. Since they are folded to become especially narrow towards their tips, this seems to conduct some of this nectar onto the surrounding surface of the corolla.



Fig. 20.39. *T. herrei*, Kennedy, north of Jakkalswater (photo: H.C. Kennedy).

TROMOTRICHE HERREI

In *T. herrei* each inner lobe is much swollen and rounded towards the apex and is shiny, almost black and smooth. Each has a very similarly shaped, though slightly smaller and quite obviously laterally flattened dorsal horn. Together these parts of the inner corona fill the base of the tube and markedly restrict access to the pollinia and guide-rails. In many details the gynostegium bears a remarkable resemblance to that of *Stapelia clavicorona* (where gaining access to the pollinia is also quite difficult) but this is a case of convergence and the two are not closely related.

History

Tromotriche herrei was discovered by Adolar Gottlieb Julius 'Hans' Herre near Eksteenfontein (formerly Stinkfontein) during his second expedition to the Richtersveld, in October 1930. During this expedition he also collected material of the same species at Hellskloof (north of Kubus) which Nel named *Stapelia tigrina*. *Stapelia tigrina* Nel was later named *S. neli-ana* by White & Sloane, since they believed that this name had been published earlier by A. Berger as a new combination for *Stapelia atrata* var. *tigrina* Rust. However, Berger (1910: 194) expressly stated that he was not making

any such combinations (see below also under 'Possible Hybrids'), so there was no need for the name *S. neli-ana*. Nel separated *Stapelia tigrina* from *T. herrei* by the longer pedicels and the

larger, darker, less rugulose and more widely opening flowers, but Leach (1980a) placed this into synonymy under *T. herrei*, which is anyway quite variable in most of these features.



Fig. 20.40. *T. herrei*, PVB 8384, Blesberg, north of Jakkalswater.



Fig. 20.41. *T. herrei*, PVB 8384, Blesberg, north of Jakkalswater.



Fig. 20.42. *T. herrei*, PVB 8384, Blesberg, north of Jakkalswater.

8. *Tromotriche baylissii*

Tromotriche baylissii (L.C.Leach) Bruyns, S.

African J. Bot. 61: 206 (1995).

Stapelianthus baylissii L.C.Leach, *J. S. African Bot.* 34:136 (1968).

Tridentea baylissii (L.C.Leach)

L.C.Leach, *Trans. Rhod. Scient. Assoc.* 59: 4 (1978).

Type: South Africa, Cape, south-eastern end of Baviaanskloof, Leach & Bayliss 13617 (PRE, holo; K, NBG, SRGH, iso).

Tridentea baylissii var. *ciliata* L.C.Leach, *Excelsa Taxon. Ser.* 2: 62 (1980).

Type: Cape, western end of Baviaanskloof, Rawlinson sub Plowes 4792 (PRE).

Succulent spreading to form loose clump or pendent from ledges on cliffs. **Stems** 40 mm-2 (-3) m long, 6-20 mm thick, prostrate or ascending then soon arching back to ground and sometimes somewhat rhizomatous, square in cross-section, blue-green; **tubercles** very obscure, without apical tooth. **Inflorescence** 1 to several, arising towards apex of stem, each bearing 1-5 flowers opening in gradual succession, flowers continuing over several seasons (as stem lengthens) on gradually lengthening peduncle 5-30 mm long; **pedicel** 12-15 mm long, 2 mm thick, ascending

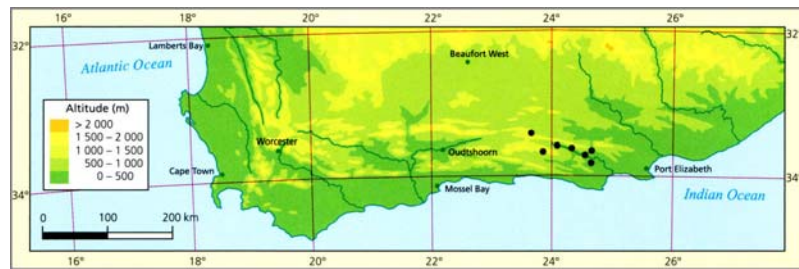


Fig. 20.43. Distribution of *Tromotriche baylissii*.

then spreading so that flower facing $\pm$ horizontally; **sepals** 2-3 mm long, 1 mm broad at base, ovate to lanceolate, acute. **Corolla** 20-25 mm diam., tubular-campanulate; outside faintly mottled with brownish to purplish pink becoming darker towards apex of lobes; inside brownish to purplish red, markedly to slightly transversely rugulose except in lower half of tube and towards tips of lobes, sometimes with small nearly spherical to clavate papillae all over; **tube** 7-15 mm long, 12-14 mm broad, strongly pentagonal to circular in cross-section, conical to nearly cylindrical, with corolla thickened in lower half except near base so that distinctly overhanging 'annulus' arises near base; **lobes** 5-8 mm long, 7-10 mm broad at base, erect

to spreading, deltate, acute, margins recurved so that inner surface distinctly convex, sometimes with clavate vibratile cilia up to 2 mm long near base. **Corona** 6-7 mm tall, 4-5 mm broad, red to purple towards extremities, yellow towards base, raised on distinct stipe becoming very broad towards base; **outer lobes** 2.0-2.5 mm long, $\pm$ 1 mm broad, ascending to erect, $\pm$ rectangular, divided in upper 1 mm into 2 erect acute teeth and a small truncate toothlet between them to truncate and finely and equally 3-toothed, deeply channelled down inner surface; **inner lobes** 4-5 mm long, adpressed to backs of anthers then erect and connivent then spreading towards apices, dorsiventrally flattened in lower $\pm$ 2 mm then terete and

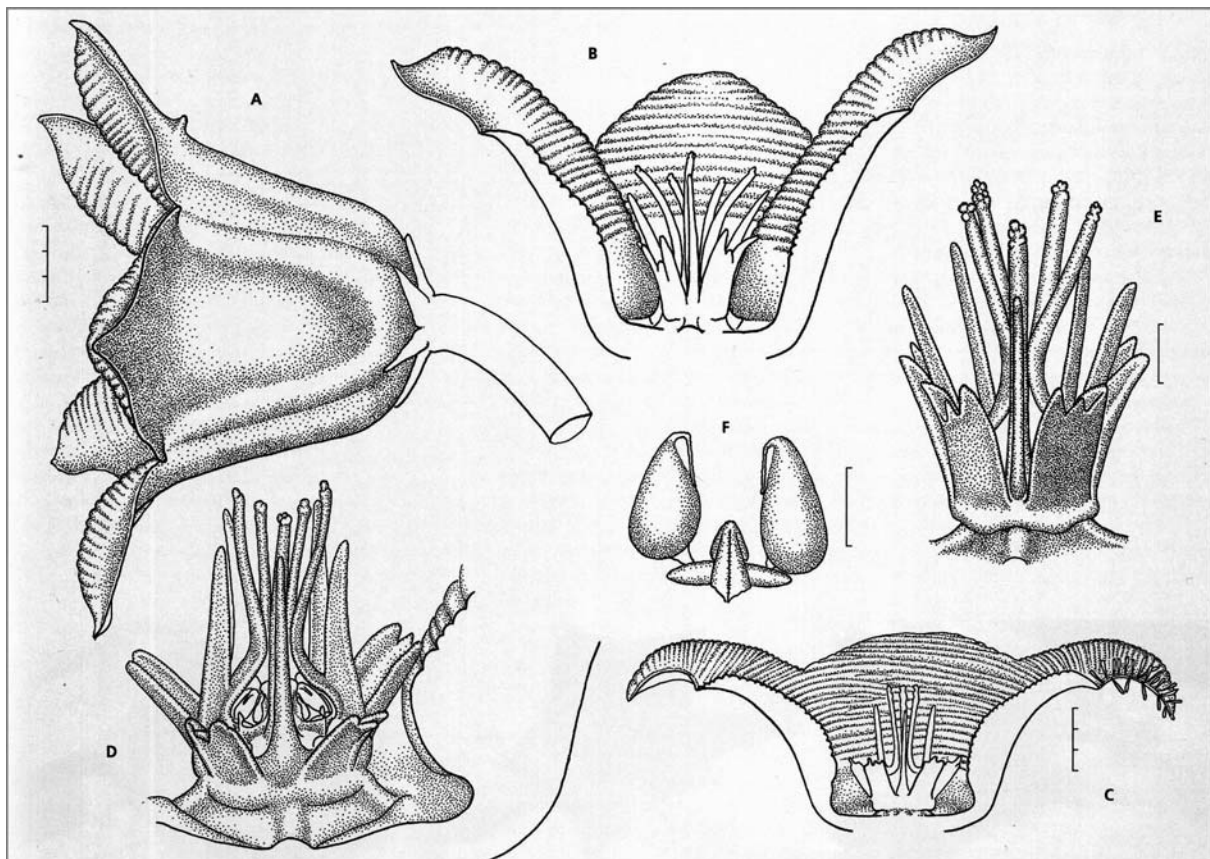


Fig. 20.44. *Tromotriche baylissii*. A, side view of flower. B, C, side view of dissected flower. D, E, side view of gynoecium. F, pollinarium. Scale bars: A, B, 3 mm; C, 3 mm; D, E, 1 mm (at E); F, 0.25 mm. Drawn from: A, B, E, F, PVB 1895, west of Patensie, eastern Baviaanskloof; C, PVB 7125, south-west of Patensie; D, PVB 1603, near Studtis, Baviaanskloof.

TROMOTRICHE BAYLISSII

filiform, somewhat rugulose at slightly clavate apex, with nearly erect slender laterally flattened obtuse dorsal horn 3.0-3.5 mm long arising near base.

Distribution and habitat

Tromotriche baylissii has been found in most of the deep kloofs in the western part of the Baviaanskloof around Studtis. It is also quite common in the eastern part of the Baviaanskloof to the west of Patensie, where again it occurs in most of the kloofs. Outside the Baviaanskloof it has been found further north along the Groot River towards Steytlerville and even in a kloof facing Steytlerville on the northern side of the Baviaanskloof Mountains. In addition, I have also found it rather sporadically along the Kouga River in the hills adjoining the Long Kloof.

Plants almost always grow in accumulations of soil and leaf-litter on small ledges on sandstone cliffs, often in exceedingly precipitous and inaccessible places. Very occasionally plants have been found among bushes and rocks in steep but not precipitous places.

Diagnostic features and relationships

As a consequence of their habitat, plants are usually found with at least some pendulous stems, which may reach the remarkable length of nearly 3 m. Usually, though, they are of quite modest dimensions and more commonly reach lengths of 0.3 - 1.0 m. Plants growing among bushes in steep areas have the prostrate habit with somewhat 'burrowing' stems that one finds more frequently in *T. choanantha*.

The stems are more or less square in cross-section with low, obscure tubercles forming the angles and the tissue slightly concave between these angles. Younger plants are bluish green but much older pieces can become covered with a grey, corky layer.

Flowers of *T. baylissii* are produced mainly towards the apices of the stems, particularly on young growth and they are held on a spreading pedicel so as to face horizontally. Like those of *T. choanantha*, they are shaped very like a bell and give off a light, foul odour. The outside is brownish, sometimes faintly mottled, shiny

and usually slightly (sometimes very strongly) pentagonal towards the base with the corners alternating with the lobes. Inside, the corolla is brownish red and transversely rugulose, especially around the middle of the tube, but these ridges become fainter suddenly near the base and also gradually fade out on the lobes. In some flowers there are also five radial grooves running down from below the middle of each lobe and these give the inside of the tube a distinctly pentagonal shape too but, because of the thickness of the corolla lower down, this does not correspond with the five-sidedness of the corolla outside.

If the corolla is cut lengthwise, it can be seen that the tube thickens noticeably towards the base and then very suddenly narrows again so as to form an overhanging ledge above a small wider area around the base of the gynostegium. This ledge is the equivalent of the annulus in species such as *T. revoluta*.

The corona lobes fit snugly into the lower part of the tube where it is thickest. Here the outer lobes rise quite steeply, pressing against the side of the tube and nestling into the grooves running down it. They are relatively short and deeply channelled down the inner surface. Since the outer lobes are fairly steeply inclined, the area around the guide-rails is very restricted and it is quite difficult to gain access to them. The pollinia are suitably shaped for this, though, being much narrower and longer than in any other *Tromotriche* (except *T. choanantha*) and consequently they are able to fit into this restricted space. This restriction of the space around the guide-rails may also be seen in *Orbea carnososa* and *Stapelia flavopurpurea*. Beyond the anthers the inner lobes rise in the centre and are often gathered into a column. They are slender and cylindrical, with a slightly roughened and swollen apex. Each lobe has a comparatively large, laterally flattened, dorsal horn which is nearly as long as the lobe itself and rises steeply just behind it.

The flowers in *T. baylissii* vary greatly in the breadth of the tube towards its mouth, its depth and the extent to which it is pentagonal. The photographs by G.G. Smith of Marjorie Courtenay-Latimer's collection (NBG records) show a flower which is very wide at the mouth

and relatively shallow (as well as very boldly rugulose inside) whereas Leach's photographs (Leach 1968), of plants found in much the same area, show flowers which have a much deeper and narrower tube, with much shallower rugosities inside. Similar variation in the shape of the flower is known in *T. choanantha*.

Leach (1980a) described a 'var. *ciliata*' for plants with cilia on the margins of the corolla lobes. At that time such plants were known only from around Studtis. More recently they have also been collected from cliff faces near Andrieskraal at the eastern end of the Baviaanskloof and some plants from south of Steytlerville also have ciliate flowers, growing with others without them. It seems therefore that these marginal cilia are of sporadic occurrence throughout the distribution of the species. In several species of *Stapeliad* (e.g. *Duvalia caespitosa*, *T. choanantha*), cilia are variably present on the margins of the lobes and, now that it has been established to occur more widely in *T. baylissii*, there is no reason to recognise this variation taxonomically.

History

Tromotriche baylissii was first recorded by the redoubtable Marjorie Eileen Doris Courtenay-Latimer (24 February 1907-17 May 2004). Ms Courtenay-Latimer was at one time the curator of the East London Museum, which she established from her family's own collection, and she was the co-discoverer in December 1938 of the coelacanth, a rare marine fish which, until then, had only been known from fossils. On 5 March 1948 she gathered some plants of *T. baylissii* at the eastern end of the Baviaanskloof near Patensie, on the farm Mistkraal. Like several other species that were then undescribed, nothing was done about it until R.D.A. Bayliss brought it to the attention of Leach, who finally described it in 1968 as a species of *Stapelianthus*.

At the time of Leach's account of *Tridentea*, 'only three populations (possibly only two)' (Leach 1980a: 62) were known. However, it has now been established as being quite widespread in the Baviaanskloof and Groot Winterhoek Mountains.



Fig. 20.45. *T. baylissii*, PVB 6325, south of Steytlerville. Plants with relatively narrow corolla with ciliate lobes.



Fig. 20.46. *T. baylissii*, PVB 1895, west of Patensie in eastern part of Baviaanskloof, plants with fairly broad corolla but the lobes not ciliate.



Fig. 20.47. *T. baylissii*, PVB 7125, south-west of Patensie. Here plants also have quite broad flowers but the lobes are mostly ciliate.



Fig. 20.48. *T. baylissii*, PVB 1603, near Studtis, Baviaanskloof, plant hanging for about 2 m from cliff in sheltered kloof, December 1977.

9. *Tromotriche choanantha*

Tromotriche choanantha (Lavranos & H. Hall)

Bruyns, S. *African J. Bot.* 61: 204 (1995).

Stapelia choanantha Lavranos & H. Hall, *J. S. African Bot.* 30: 107 (1964).

Stapelianthus choananthus (Lavranos & H. Hall)

R.A.Dyer, *Fl. PL Africa* 37:t.1459 (1966).

Tridentea choanantha (Lavranos & H. Hall)

L.C. Leach, *Trans. Rhod. Scient. Assoc.* 59: 4 (1978).

Type: South Africa, Cape, Huis River Pass, Hail 2579 (BOL).

Succulent spreading to form loose clump or pendent from ledges on cliffs. **Stems** 40 mm–2 m long, 6–12 mm thick, prostrate or ascending then soon arching back to ground and sometimes somewhat rhizomatous, usually purple-green; **tubercles** very obscure so stem obscurely and very obtusely 4-angled to almost cylindrical, without apical tooth. **Inflorescences** 1 to several per stem arising towards base of young stems, each bearing 1–5 flowers developing in gradual succession on stout peduncle up to 5 mm long (while stem still short, usually becoming inactive once stem elongates); **pedicel** $\pm$ 10 mm long, 1.5 mm thick, spreading with slightly descending apex so

that flower facing horizontally or slightly nodding; **sepals** 2.5–3.5 mm long, 1 mm broad at base, lanceolate, acute. **Corolla** 20–25 mm diam., tubular-campanulate; outside pink towards base becoming maroon above middle and on lobes, usually with 1 outstanding vein on each lobe; inside dark maroon, smooth; **tube** 11–16 mm long, 10–12 mm broad, distinctly pentagonal, conical to nearly cylindrical, with corolla thickened in lower half except near base so that overhanging 'annulus' arises near base; **lobes** 5–6 mm long, 7–8 mm broad at base, erect to spreading, deltate, acute, very slightly convex on inner surface but margins not reflexed, eciliate or very rarely with vibratile flattened cilia $\pm$ 1.5 mm long near bases. **Corona** $\pm$ 8 mm tall, 4–5 mm broad, maroon, raised on distinct stipe almost 1 mm long; **outer lobes** 2.5–3.0 mm long, $\pm$ 1.2 mm broad, nearly erect, $\pm$ rectangular, divided in upper 1 mm into 2 erect acute teeth and a small truncate toothlet between them to truncate and finely and equally 3-toothed, deeply channelled down inner surface; **inner lobes** 5–6 mm long, adpressed to backs of anthers then erect and connivent then spreading towards apices, dorsiventrally flattened in lower $\pm$ 1 mm then terete and filiform, obtuse to very slightly rugulose at apex, with nearly erect slender laterally flattened obtuse dorsal horn 3.0–3.5 mm long arising near base.



Fig. 20.49. Distribution of *Tromotriche choanantha*.

Distribution and habitat

Tromotriche choanantha occurs in the mountainous terrain around the small town of Calitzdorp in the Little Karoo. Plants have been found in the Huis River Mountains to the west and south-west of Calitzdorp, in the Swartberg as far west as Seweweekspoort and along the Gamka River and also in the Rooiberg to the south of the town.

In general, specimens grow on ledges on very steep to vertical sandstone faces in sheltered and sometimes quite densely wooded gorges. Plants are by no means

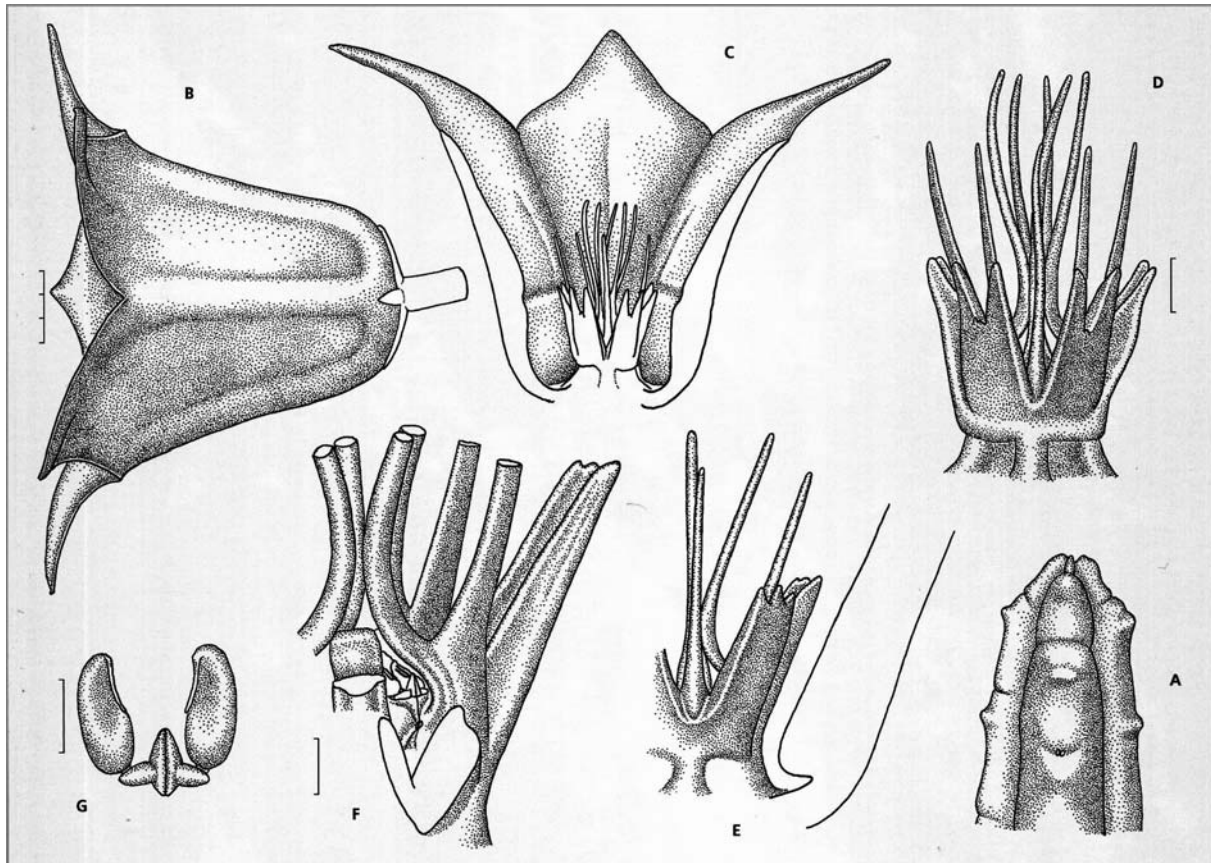


Fig. 20.50. *Tromotriche choanantha*. A, apex of stem. B, side view of flower. C, side view of dissected flower. D, side view of gynostegium. E, part of centre of dissected flower showing thickened 'annulus' above base, also rather different outer corona lobes to D. F, gynostegium with one outer and one inner corona lobe excised. G, pollinarium. Scale bars: A–C, 3 mm (at B); D, E, 1 mm (at D); F, 1 mm; G, 0.25 mm. Drawn from: A–C, E, F, PVB 2216, Huis River Pass; D, G, PVB 2907, Gamka Poort.



Fig. 20.51. *T. choanantha*, PVB 8422, near Zoar.



Fig. 20.52. *T. choanantha*, PVB 8422, near Zoar.



Fig. 20.53. *T. choanantha*, PVB 3728, south of Calitzdorp, in habitat, April 1989.a

always pendulous from cliffs. However, they seem to prefer to grow in or very near steep to precipitous spots. Here good drainage and shallow soils probably contribute to very local, high aridity while temperatures do not rise too high because of circulation of air up such steep spots. In these ravines, there is also very little direct sun which could burn the plants' long, exposed stems. Specimens were quite often found spreading on ledges with their stems burrowing beneath the surface wherever possible and only those stems that happen to grow over the edge of a ledge become pendent.

Diagnostic features and relationships

Tromotriche choanantha and *T. baylissii* are very closely related (a fact that is borne out by molecular data as well) and both inhabit similar terrain. The stems of both species are similar to those found throughout *Tromotriche*. Their very obscure tubercles, more or less without an apical tooth, lend them a characteristically rounded appearance. Florally these two species appear superficially to be very different from others in *Tromotriche* with their purple-red, tubular-campanulate flowers. However, the corona is similar to that of *T. revoluta* (inclusive of the clavate tips of the inner corona lobes in *T. baylissii*) except for the fact that the outer lobes ascend rather than spread, clearly to fit into the fairly narrow corolla tube.

In some plants collected near Zoar (PVB 8422), the margins of the corolla lobes have fine flattened, vibratile cilia, while others from the same locality are without these cilia. The corolla lobes in this species are far more rarely ciliate than in *T. baylissii* and so far this is the only locality where this has been observed in *T. choanantha*.

Tromotriche choanantha differs from *T. baylissii* in a few respects. It has noticeably more rounded stems; flowers are produced only near the bases of the stems and each inflorescence bears flowers only once, not over several seasons as in *T. baylissii*; the inside of the flower is smooth rather than transversely rugose. There is also a slight difference in the



Fig. 20.54. *T. choanantha*, St Helena, Calitzdorp, in habitat among rocks and leaf-litter on steep slope, October 2003.

TROMOTRICHE CHOANANTHA

inner corona lobes which are more obviously thickened at the apices in *T. baylissii* than in *T. choanantha*. In *T. baylissii* the apices are also somewhat tuberculate whereas they are smooth in *T. choanantha*. The suggestion has been made (M. Bruce Bayer in NBG archives) that *T. baylissii* and *T. choanantha* belong to a single species and this is not unreasonable.

History

The first recorded gathering of *T. choanantha* is that of P.O. le Roux, which was made in 1937 somewhere near Calitzdorp. This material was grown at Kirstenbosch and, on flowering in September 1938, a minute specimen was made and deposited in the Bolus Herbarium. At some stage N.S. Pillans saw this plant and suggested calling it '*Stapelia serpentina*' but he was otherwise occupied and never got as far as publishing this. It was again recorded by L.J. Bredell in 1944 from the Huis River Mountains near Calitzdorp. He seems to have given a specimen to Mrs. H. Blackburn of Calitzdorp and again a few minute scraps were deposited in the Bolus Herbarium.

Tromotriche choanantha was rediscovered in September 1962 by a group of three young naturalists, Peter H.C. Salter, Alfred Möller and Bruce Ramsey, who found it in a gorge in the Huis River Pass and brought some pieces to H. Hall at Kirstenbosch. Hall and R.D.A. Bayliss later visited the locality where it had been found and, from the collection they then made, it was finally described in 1964.

As in the case of *Orbea longii*, this species was also, until recently, only known from the type locality (Leach 1980a). My own researches have shown that it occurs in several other similar gorges in the Huis River Mountains both west and south-west of Calitzdorp, as well as somewhat further north along the Gamka River and south of Calitzdorp in similar kloofs in the northern slopes of the Rooiberg. Many of the deep ravines in this area are of very difficult access and it probably occurs in most of them.

Although it has not been tossed around among quite as many genera as *T. aperta*, in the short time since it was described, *T. choanantha* has still belonged to surprisingly many genera. According to its original authors, the corona clearly placed it in *Stapelia* but was nevertheless different from that in all other members of *Stapelia*. They suggested that it showed some similarities to *Stapelia* (now *Tromotriche*) *revoluta*.

Dyer (1965) felt that across the *stapeliads* the corona was too variable to be of taxonomic significance and that the shape of the corolla should be emphasised more. He noticed some similarities between the buds of *S. choanantha* and *Stapelianthus decaryi* and placed *S. choanantha* in *Stapelianthus* largely on the basis of this.

Rauh & Wertel (1968) examined the situation again and pointed out that it is unwise to define relationships between species purely on similarities in the buds without checking whether there are further similarities elsewhere in the flower. Furthermore, since the genus *Stapelianthus* was otherwise confined to Madagascar, they argued that it would be very remarkable if a species also occurred in the southern Cape (though such disjunctions exist in the Apocynaceae, as is well known in *Pachypodium* (Uhlarz 1974b) and *Ceropegia*

(Meve & Liede 1994a)). Rauh & Wertel found that *S. choanantha* was a typical *Stapelia* and they observed that any resemblance of the buds in *S. choanantha* to those in *Stapelianthus decaryi* was relatively vague and apparently fortuitous, since it was not substantiated by any further similarities. Leach (1978b) moved it together with several other species to *Tridentea* and it was only in 1995 that the possibility that it was closely allied to *Tromotriche revoluta* was reconsidered and found to be likely, resulting in both species belonging to the genus *Tromotriche*.



Fig. 20.55. *T. choanantha*, PVB 2218, south-west of Calitzdorp, growing here with *Crassula rupestris* subsp. *marnieriana*, in habitat, February 2000.

21. Hybrids

Intergeneric and interspecific hybrids have appeared in cultivation since stapeliads were first grown in Europe. Several of the 'species' illustrated by Jacquin (1806-19) seem to be hybrids and these have continued to feature, so that even White & Sloane (1937) described a few. Such plants arose from fortuitous pollinations by flies in the greenhouse and often involve species that do not occur together naturally. An example of this is provided by *Orbea maculosa*, which at one time was quite plentiful in European collections and is probably the cross *Orbea variegata* X *Tromotriche revoluta*. With the increased understanding of the mechanism of pollination, it has been possible to produce hybrids at will and Barad has shown that practically any two stapeliads, however distantly related, can be crossed (Barad 1990). Walker (1988) even documented a cross which involved *Brachystelma barberae* and possibly a *Stapelia*.

N.E. Brown (1890) reckoned that many of the species of stapeliad had arisen through hybridisation. This view was challenged by Gravely & Mayuranathan (1931), based on their field experience, and there is no evidence for it today either. Two species that might be of hybrid origin are *Huernia praestans* and *Orbea pulchella*, but experiments aimed at producing them artificially have not been successful.

Stapeliads often grow socially in habitat and three to six or more species from different genera may be found within a few meters of one another. Despite this frequent gregariousness, hybrids between them are quite rare. In a few localities several hybrids have been seen. The best example of this is in the vicinity of the Calitzdorp Dam where, in a relatively small area, *Huernia barbata* X *H. pillansii* (Bruyns 1978), *Duvalia caespitosa* X *H. barbata* (Bruyns 1981b) and *H. barbata* X *H. guttata* have all been observed. Hybrid plants are generally solitary. Occasionally, though, whole swarms of them have been detected, as was reported for a probable cross between *Hoodia flava* and *H. gordonii* (Bruyns 1980). Here many plants of this hybrid were seen, though they have since all vanished from the spot (though it has been seen elsewhere, fig. 21.1). Specimens of this hybrid were fertile and back-crosses with its putative parents were also collected there. It seems that in the case of *Lückhoffia beukmanii* several plants were also found (White & Sloane 1937). Several putative hybrids have been collected repeatedly, though invariably just as single plants. This is the case for what may be *Echidnopsis atlantica*, for *Hoodiopsis triebneri*, *Huernia distincta*, *Tavaresia meintjesii* and for *T. thompsoniorum*. This repeated occurrence usually reflects the wide sympatry of the putative parents.

Perhaps the greatest problem posed by these hybrids is their parentage. The methods perfected by M. Bruce Bayer at the Karoo Gar-

den, Worcester, and by Barad in New Jersey have been used to test the postulated parentage of a few of them. Barad synthesised the hybrid *Hoodia officinalis* subsp. *deletaiana* X *Tromotriche ruschiana* (Barad 1989). This was suspected of being the parentage of a singular plant that he had personally collected in the Klinghardt Mountains of southern Namibia (Barad & Lavranos 1978) and his experiments showed this suspicion to have been correct. It seems probable that this is the same as the unusual plant named *Echidnopsis atlantica* by Dinter, which he had discovered in the same area in September 1922 (Dinter 1923). Bayer investigated the case of *Stapelia erectiflora* var. *prostratiflora*, which he showed to be a hybrid between *S. erectiflora* and *S. glanduliflora* (Bayer 1986). He also investigated *Huernia distincta*. This was surmised to be a hybrid between *H. barbata* and *H. distincta* by N.S. Pillans, who had discovered it two miles east of Matjiesfontein in January 1904. It was gathered in the same area in 1926 and in 1933 by Archer and has continued to be collected occasionally (Leach 1976a, Bruyns 1981b), but generally only as solitary individuals and often associated with its putative parents. Bayer showed that it was indeed the cross *H. barbata* X *H. pillansii* (Leach 1988).

Altogether a considerable number of naturally occurring, putative intergeneric and interspecific hybrids are known in southern Africa and some examples are shown here. Giess (1974) reported two unusual ones from Namibia. One of these was, again, a fertile interspecific *Hoodia*-cross, also between a large-flowered and a small-flowered species. Plowes (1978b) reported several from Zimbabwe. Leach (1969a) reported several hybrids which had been gathered in Zimbabwe and which involved *H. verekeri* as one parent. He also discussed the probable hybrid origin of *Huernia schneideriana* A.Berger, which originated from a single collection made in southern Tanzania. A hybrid swarm involving *Huernia hislopianii* and *H. leachii* is also known in Moçambique. Further afield, possible hybrids were reported in India by Gravely & Mayuranathan (1931) between the varieties of *Caralluma adscendens*. However, there is a remarkable lack of any such reports from north-east Africa and southern Arabia, where stapeliads occur in substantial numbers, although the collecting that has taken place there has perhaps been too superficial to have detected them. In this region the only documented case is a hybrid between two species of *Echidnopsis* which was found by M.G. Gilbert in eastern Ethiopia (Bruyns 1988).

According to the International Code of Botanical Nomenclature, intergeneric hybrids should be named. However, the frequent changes among generic names that have taken place over the past few decades, coupled with

the very rare occurrence of these hybrids, makes this practice somewhat pointless. Those from southern Africa that have at some time received a binomial name are listed below.

Duvalia caespitosa X *Piarranthus punctatus*

X *Duvaliaranthus albostratus* Bruyns, J. S. *African Bot.* 42: 365 (1976).

Type: South Africa, Cape, foot of Vanrhyn's Pass, Vierfontein, Bruyns 91/75 (NBG).

Hoodia gordonii X *Orbeopsis lutea* subsp. *vaga* (Bruyns 1993)

Hoodiopsis triebneri C.A.Lückh., S. *African Gard. & Country Life* 23: 231 (1933).

X *Hoodialluma triebneri* G.D.Rowley, *Rept. Pl. Succ.* 27: 4 (1976).

Type: Namibia, *Triebner sub Lückhoff* 183 (missing).

Lectotype: S. *African Gard. & Country Life* 23: fig.

H. triebneri var. *ciliata* C.A.Lückh, in A.C. White & B. Sloane, *Stap.*, ed. 2, 3:1144 (1937).

Type: Namibia, *Triebner* (missing).

Lectotype (selected here): White & Sloane, *Stap.*: fig. 1170.

Hoodia gordonii X *Stapelia arenosa* (Bruyns 1993)

Stapelia beukmanii C.A.Lückh., S. *African Gard. & Country Life* 24:101 (1934).

Lückhoffia beukmanii (C.A.Lückh.) A.C. White & B.Sloane, S. *African Gard. & Country Life* 25: 37 (1935).

X *Hoodiapelia beukmanii* (C.A.Lückh.) G.D.Rowley, *Rept. Pl. Succ.* 27: 4 (1976).

X *Hoodiostemon beukmanii* (C.A.Lückh.) P.V.Heath, *Calyx* 1: 20 (1992).

Type: South Africa, Cape, near Doringbos, *Beukman sub Lückhoff* 191 (BOL).

Hoodia officinalis subsp. *deletaiana* X

Tromotriche ruschiana (Barad & Lavranos 1978, Barad 1989)

? *Echidnopsis atlantica* Dinter, *Feddes Rept. Spec. Nov. Regni Veg.* 30:191 (1932).

X *Trichodentea atlantica* (Dinter) P.V.Heath, *Calyx* 1:20 (1992).

Type: Namibia, Klinghardt Mountains, *Dinter* (missing).

The identity of Dinter's plant remains uncertain, as the single plant that he found died in cultivation in Lichtenstein (near Windhoek, Namibia) before it flowered.

Huernia barbata X *Huernia pillansii* (Leach 1988)

Huernia distincta N.E.Br., Fl. Cap. 4 (1): 910 (1909).

Type: South Africa, Cape, Matjiesfontein, N.S. Pillans 83 (K, holo; BOL, iso).

It is interesting that Pillans remarked on the type sheet in the Bolus Herbarium that 'I have only been able to find one large clump. It seems to me to be a natural hybrid between *H. pillansii* and *H. clavigera* which bound it on both sides. Nevertheless it is a species, well defined.'

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Quaqua framesii X *Quaqua pulchra* (Bruyns 1999a)

Q. albersii Plowes, *Excelsa* 16: 94 (1994).

Type: South Africa, Cape, near Hol River, Albers 2252 (SRGH).

Stapelia erectiflora X *Stapelia glanduliflora* (Bayer 1986)

S. erectiflora var. *prostratiflora* L.C.Leach, *S. African J. Bot.* 3: 178 (1984).

Gonostemon erectiflorus f. *aberrans* P.V.Heath, *Calyx* 1:19(1992).

Type: South Africa, Cape, between Clanwilliam and Klawer, *Stayner* sub *Leach* 15724 (PRE, holo; NBG, iso).

Stapelia gigantea X *Orbea caudata* subsp. *rhodesiaca* (Leach 1973)

Stapelia tarantuloides R.A.Dyer, *Fl. PL South Africa* 18: t. 717 (1938).

X *Carapelia tarantuloides* (R.A.Dyer) G.D.Rowley, *Repert. PL Succ.* 23: 6 (1972).

X *Orbeopelia tarantuloides* (R.A.Dyer) G.D.Rowley, *Cact. Succ. J. Gr. Brit.* 44: 2 (1982).

X *Orbeostemon tarantuloides* (R.A.Dyer) P.V.Heath, *Calyx* 1:20 (1992).

Type: Zimbabwe, ± 80 km west of Gwanda, S. Thompson sub *PRE* 24162 (PRE).

Stapelia kwebensis X *Orbea caudata* subsp. *rhodesiaca* (Leach 1973)

X *Orbeostemon leachii* P.V.Heath, *Calyx* 1: 21 (1992)

Stapelia kwebensis X *Orbea maculata* subsp. *maculata* (Leach 1985)

X *Gonostapelia plowesii* P.V.Heath, *Calyx* 1: 21 (1992)



Fig. 21.2. *Duvalia caespitosa* X *Piранthus punctatus*, PVB 91/75, foot of Vanrhyn's Pass, Vierfontein, (*Duvaliaranthus albostratus*).



Fig. 21.4. *Hoodia officinalis* subsp. *delaetiana* X *Tromotriche ruschiana*, Hammer, Klinghardt Mountains, south of Lüderitz, Namibia (? *Echidnopsis atlantica*).

Stapelia gigantea X *Stapelia gettliffei* (Leach 1980b, 1985)

Stapelia meintjesii I.Verd., *Fl. PL South Africa* 23: t. 917 (1943).

Gonostemon X *meintjesii* (I.Verd.) P.V.Heath, *Calyx* 1:19(1992).

Type: Meintjes sub *PRE* 27144 (PRE).

Stapelia hirsuta X *Orbea namaquensis* (Leach 1985)

Stapelia barklyi N.E.Br., *Hooker's Icon. PL* 20:t.1909 (1890).

X *Orbelia barklyi* (N.E.Br.) G.D.Rowley, *Cact. Succ. J. Gr. Brit.* 44: 2 (1982).

X *Gonostapelia barklyi* (N.E.Br.) P.V.Heath, *Calyx* 1:21(1992).

Type: South Africa, Cape, near Springbok, Morris sub *Barkly* 31 (missing).

It is possible that this 'species' caused N.E. Brown to abandon any ideas that he might have entertained about splitting up the genus *Stapelia*, since it shares many characters of the two genera *Stapelia* and *Orbea* as they are now recognised.

Stapelia kwebensis X *Stapelia schinzii* (Giess 1974)

Gonostemon X *giessii* P.V.Heath, *Calyx* 1: 20 (1992).

Stapelia pillansii (?) X *Tridentea gemmiflora* (Leach 1985).

Stapelia bijliae Pillans in A.C. White & B. Sloane, *Stap.*, ed. 2, 2: 674 (1937).

X *Gonodentaea bijliae* (Pillans) P.V.Heath, *Calyx* 2: (1993).

Type: South Africa, Mossel Bay, D. van der Bijl 6 (BOL).



Fig. 21.3. *Hoodia gordonii* X *Orbea lutea* subsp. *vaga*, PVB 3542, eastern foot of Great Karas Mountains, Namibia (*Hoodiopsis triebneri*).



Fig. 21.5. *Huernia guttata* subsp. *guttata* X *H. barbata* subsp. *barbata*, Calitzdorp Dam.



Fig. 21.1. *Hoodia gordonii* X *Hoodia flava*, PVB 7965, east of Loeriesfontein.

Tavaresia barklyi X *Huernia urceolata* (?)

Tavaresia thompsoniorum Van Jaarsveld & Nagel, *Asklepios* 76: 9 (1999) as *T. thompsonii* emend. Jonkers (1999).

Type: Angola, between Iona and *Oncocua* near Abamalinda Mtn, Bell (NBG, missing).

'*Tavaresia thompsoniorum*' was described from a single plant collected by Clare Bell in southern Angola in July 1996. Another very similar-flowered plant was found in January 1993 along the Kunene River east of Epupa Falls in Namibia {PVB 5603a}. In this case also only a single specimen was found, in this instance growing with *Tavaresia barklyi*, *Hoodia parviflora* and *Huernia urceolata*. A similar plant was recorded under *Hoodiopsis* in Jacobsen (1960: 614-5) and this had been collected by Wilhelm Triebner, ostensibly in Ovamboland. The very sporadic occurrence of this plant suggests that it is a hybrid but, at this stage, the parentage remains uncertain.

Tavaresia barklyi X *Stapelia gettliffei* ? (Leach 1974b, 1985)

Tavaresia meintjesii R.A.Dyer, *Bothalia* 6: 415 (1954).

Decabelone meintjesii (R.A.Dyer) G.D.Rowley, *Natl Cact. Succ. J.* 13: 78 (1958).

X *Staparesia meintjesii* (R.A.Dyer) G.D.Rowley, *Natl Cact. Succ. J.* 37: 79 (1982).

X *Tavastemon meintjesii* (R.A.Dyer) P.V.Heath, *Calyx* 1:21(1992).

Type: South Africa, Transvaal, ± 20 miles east of Messina, Myburgh sub *Meintjes* 663 (PRE).

Although it seems that this hybrid has still not been artificially synthesised to determine its true parentage, it is reasonable to assume that it is not a species of *Tavaresia* but a hybrid with the above parentage. It was figured in detail by Alp (1989).



Fig. 21.6. *Huernia praestans* X *Duvalia parviflora*, PVB 6305a, west of Ladismith.



Fig. 21.7. *Huernia pillansii* X *Duvalia caespitosa* subsp. *caespitosa*, PVB 1213, Calitzdorp Dam.



Fig. 21.8. *Huernia humilis* X *Duvalia corderoyi*, PVB 5971b, south-west of Fraserburg.



Fig. 21.9. *Huernia hystrix* subsp. *hystrix* X *Duvalia polita*, G. Marais, west of Mara siding, near Louis Trichardt.



Fig. 21.10. *Huernia pillansii* X *H. barbata* subsp. *barbata*, PVB 3059, south-east of Rooinek Pass (*Huernia distincta*).



Fig. 21.11. *Huernia humilis* X *H. barbata* subsp. *barbata*, PVB 5971a, south-west of Fraserburg.



Fig. 21.12. *Huernia leachii* X *H. hislopilii* subsp. *hislopilii*, PVB 7400, south of Chimoio, Manhica Province, Moçambique.

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Fig. 21.13. *Quaqua acutiloba* X *Q. mammillaris*, Nagel, north-west of Calvinia.



Fig. 21.14. *Tavaresia barklyi* X *Huernia urceolata* ?, PVB 5603a, along the Kunene River east of Epupa Falls, Namibia (*Tavaresia thompsoniorum*).

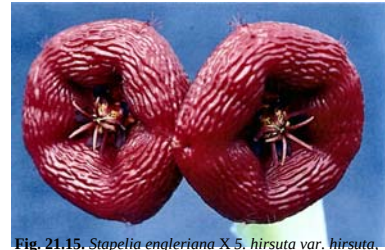


Fig. 21.15. *Stapelia engleriana* X *S. hirsuta* var. *hirsuta*, PVB 3709, east of Seweweekspoort.



Fig. 21.16. *Stapelia engleriana* X ??, PVB 5068, west of Rietbron, Namibia with *Stapelia erectiflora* var. *prostratiflora*. *Stapelia erectiflora* X *S. glanduliflora*, PVB 1289, Doom River Bridge, with tessellate 6-angled stems possibly involving *Quaqua arenicola*, discovered by the late Jaap and Kila Snyman.



Fig. 21.18. *Stapelia hirsuta* var. *hirsuta* X *Orbea namaquensis*, Liltved, Wildeperdehoek Pass (photo W.R. Liltved, *Stapelia barklyi*).



Fig. 21.19. *Quaqua bayeriana* X *Q. incarnata* subsp. *hottentotorum*, Wildeperdehoek Pass.

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